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*A quarterly devoted  
to malacology.*



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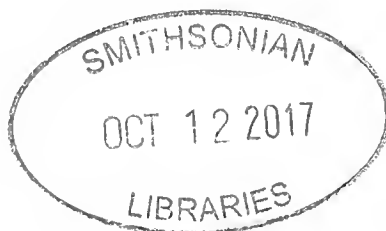
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# *Nemocataegis*, a new genus and two new species of relictual seguenzioid gastropods (Vetigastropoda: Cataegidae) and a geobiological framework for integrating patterns in Deep Marine Wallacea

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## ABSTRACT

*Nemocataegis* new genus, type species *N. mcleani*, is proposed for two elaborately sculptured, small-shelled cataegid gastropods from separate deep-water basins in the Indonesian biogeographic realm of Wallacea. The type species is from 885 m in the Gulf of Bone, between the southern and southeastern arms of Sulawesi where the narrow gulf opens into the Flores Sea. The second species, *N. quinni*, is from 503 m in the Molucca Sea adjacent to Halmahera. Both species have the oblique, broadly expanding aperture, fluted outer lip and strong spiral cords characteristic of *Cataegis* McLean and Quinn, 1987, but shells are smaller (<20 mm) and the spiral cords are densely nodose, with fine axial ribs connecting the nodes and a unique microsculpture of fine threads and intritacals in the channels between node rows. A previously described true *Cataegis* is endemic to the Makassar Strait in Wallacea, occurring at depths in excess of 1000 m. Cataegidae is re-diagnosed to include two genera, six nominal living species and two nominal fossil species. The family is assigned to Seguenzioidea based on a combination of morphological and molecular data. The new genus is endemic to Deep Marine Wallacea, and the new species occur in geographically isolated basins. Along with previously described deep-water gastropods in geologically ancient clades, they contribute to evidence of relictual biotas. The biogeographic patterns are correlated with factors that include the tracks of collecting expeditions, submarine topography, biogeographic lines, patterns of oceanic circulation, distribution of volcanic arcs and subduction zones, and major structural features resulting from tectonic collision, fragmentation, suturing, deformation, and extension over a period of more than 50 million years.

**Additional Keywords:** Sulawesi, Halmahera, Molucca Sea, Makassar Strait, Banda Arc, biogeography, hydrocarbon seep, deep sea, endemism, biogeography, systematics.

## INTRODUCTION

This is the third in a series of papers describing unusual and relatively large-shelled (>20 mm) deep-water (200–2000 m) gastropods from three basal vetigastropod families.

Remarkably, the specimens are from expeditions and museum collections in which they may have been so unusual that they were incorrectly filed, misidentified, or simply waiting for resolution of the confused state of the taxonomy of fossil and living basal gastropods that have been variously arranged under many names at the “archaeogastropod” grade of evolution.

The first paper in the series (Hickman, 2012) described a new genus and two new species in the family Gazidae Hickman and McLean, 1990. It included anatomical and radular features as well as new shell characters. The second paper (Hickman, 2016) described eight species in the family Calliotropidae Hickman and McLean, 1990. Both papers are focused on the Indo-West Pacific Region and explore the complex geologic history of tectonic plate interactions, arc volcanism, subduction, accretion, and hydrography that identify a marine geobiogeographic realm designated here as “Deep Wallacea.”

Deep Wallacea is distinct from the original terrestrial biogeographic concept that originated with Alfred Russel Wallace when he drew his famous line. Ironically, the region between Wallace’s Line and Weber’s Line was named “Wallacea” by geologist and paleontologist Roy Ernest Dickerson in an overlooked paper (1924: 3, fig. 1) designating “(1) the Asian (Sunda) Shelf, (2) Wallacea, and (3) the Australian Sahul Shelf (as) the three well-defined divisions of the Australasian Mediterranean Sea.”

The primary objective of this paper is taxonomic: to describe a new genus and two new species of extant deep-water cataegid gastropods and to revise the diagnosis of the family. A secondary objective is to provide a set of maps and discussion of factors correlated with the disjunct and relictual distribution patterns of basal marine gastropods in Deep Wallacea. These include the tracks of collecting expeditions, the path of the Indonesian Throughflow and patterns of oceanic circulation, the division of the region into many separate basins and sub-basins, the distribution of active volcanoes and volcanic arcs associated with crustal collision

and subduction, and the distribution of major structural features and terranes that record a long geologic history of dramatic change in the distribution of land and sea.

A brief background of the ecology of living cataegids, their paleontological record, and their previous classification follows as an introduction to the systematic treatment.

#### ECOLOGICAL BACKGROUND

Living cataegid gastropods have been reported previously from bathyal depths (>200 m) in two widely separated regions of the world: (1) the combined basins of the Caribbean Sea (McLean and Quinn, 1987; Warén and Bouchet, 1993, 2001; Gracia et al., 2001) and Gulf of Mexico (McLean and Quinn, 1987; Warén and Bouchet, 1993, 2001; Carney, 1994; Cordes et al., 2010) in the Americas and (2) basins in the Southwestern Pacific that include the South China Sea (Fu and Sun, 2006), Wallacean Indonesia (McLean and Quinn, 1987), and Vanuatu (Kano, 2007; Warén, 2001). Complex active tectonism in these regions has produced some of the same geologic settings and features (subduction zones, thick accretionary prisms and melange, fault zones, mud volcanoes) that in turn give rise to unusual ecological settings. While geologists have focused on fluid expulsion in these settings (sulfides, petroleum, and other hydrocarbons, especially methane), biologists have focused on the ecological communities exploiting chemical energy via chemosynthesis.

Living cataegid gastropods consistently are associated with cold seeps where conduits for sulfide- and methane-rich fluids are expelled. In these environments microbial chemosynthesis creates both a rich nutritional source and a challenging oxygen-depleted setting for development of an extremophile macrobiota. In the Gulf of Mexico cataegids are linked to specific sulfide and hydrocarbon seeps off Louisiana (Carney, 2004; Cordes et al., 2010) and in the Caribbean in the thick accretionary prism off Venezuela, Trinidad, Barbados and Colombia (Gracia et al., 2001; Gill et al., 2005).

Fluid expulsion may also include barium-rich water that precipitates at oxic/anoxic boundaries as barium sulfate and barite sheets, mounds, cones and chimneys where a cataegid is part of a unique seep community (Cordes et al., 2010). The cataegid collected in the volcanic arc of Vanuatu was associated not only with cold seeps and hydrothermal vents, but also was reported as common on sunken wood (Warén, 2011).

#### PALEONTOLOGICAL BACKGROUND

Fossil specimens all occur in cold-seep carbonates and represent a broader geographic range that includes Lower Cretaceous (Valanginian) rocks in California (Kaim et al., 2014), and Upper Cretaceous (Campanian) rocks in Japan (Kaim et al., 2009; Kiel, 2010). Kiel and Campbell (2005) note that “trochomorph” gastropods that are abundant in some Lower Cretaceous cold-seep limestones in California are difficult to classify without original shell material.

At the boundary between the South American and Caribbean plates, collection records of *Cataegis meroglypta*

are more numerous from Paleogene and Neogene seep carbonates than from modern seeps in the region (Gill et al., 2005), although this is potentially biased by greater sampling effort in the fossil record. The record of Cenozoic seep faunas in the Caribbean has been extended to sites in the Dominican Republic and Cuba (Kiel and Hansen, 2015).

The number of species is likely to increase with recognition of fossil shells described under other names in early literature. Kaim et al. (2014) note the morphological similarity of a species described as *Phasianema taurocrassum* Sacco, 1895 from the Miocene “*Calcare a Lucina*,” classic seep limestone chemoherts (Moroni, 1966; Taviani, 1994) in the Appenine chain of the Italian peninsula. Of special note is a species from Trinidad described as *Solariella godineauensis* by Katherine VanWinkle (1919), who noted (p. 26) both a flaring aperture and crenulated earinae. Kiel and Hansen (2015, fig. 14E) provide an excellent image that clearly shows seguenzioid axial threads in the interspaces between spiral cords.

#### NOMENCLATURE AND CLASSIFICATION OF CATAEGID GASTROPODS

The genus *Cataegis*, along with the family Cataegidae, is a relatively late addition to the large global inventory of vetigastropods. The family group was originally described and treated as a trochid subfamily of uncertain affinity (McLean and Quinn, 1987; Hickman and McLean, 1990; Warén and Bouchet, 1993). In a transformative, new working gastropod classification (Bouchet and Rocroi, 2005), the family was tentatively reassigned to Seguenzioidea along with Calliotropidae and Chilodontidae. This new view of Cataegidae is supported by molecular data (Kano, 2007; Kano et al., 2009; Aktipis and Giribet, 2012), although the cataegid sequence used in all three analyses (*Cataegis* sp.) is, unfortunately, not tied to a shell voucher specimen. Prior to this report there were four nominal species of cataegid gastropods, all described under *Cataegis*: two from the Caribbean (McLean and Quinn, 1987), one from Indonesia (McLean and Quinn, 1987) and one from the South China Sea (Fu and Sun, 2006).

Paleontologists have recognized fossil *Cataegis* specimens as seguenzioid without further classification (e.g. Kiel and Hansen, 2015), or with assignment to Cataeginae as a subfamily of Chilodontidae Wenz, 1938 (Kaim et al., 2009; 2014).

#### SYSTEMATICS

Subclass Vetigastropoda Salvini-Plawen, 1980  
Seguenzioidea Verrill, 1884 (unranked)  
Eucycloidea Koken, 1897 (unranked)  
Family Cataegidae McLean and Quinn, 1987

#### Genus *Cataegis* McLean and Quinn, 1987

**Type Species:** *Homalopoma finkli* Petuch, 1987 (senior synonym of *Cataegis toreuta* McLean and Quinn, 1987).

Recent, Gulf of Mexico, Caribbean and Western Atlantic; at continental slope depths, 337–1283 m.

**Remarks:** McLean and Quinn (1987) based the family group and genus primarily on a highly unusual radula in the type species. The rachidian was missing, the innermost laterals lacked cusps and were elaborately fused, and remaining three laterals had small cusps but complexly interlocking shafts and bases. Hickman and McLean (1990) suggested that the radula represented “an evolutionary excursion in the direction of disorder.” It was therefore surprising when Warén and Bouchet (1993: fig 14C) figured a radula from *C. meroglypta* McLean and Quinn, 1987 with a robust rachidian tooth with a well-developed and sharply-edged cusp. Habitat data help make sense of the radular disparity, because *C. meroglypta* occurs on hard substrates at methane seeps and feeds on bacterial films, whereas the type species is reported to feed on sunken and decaying seagrass (Warén and Bouchet, 1993). Although radular morphology is usually the best indicator of suprageneric placement, the cataegid shell is unusually rich in characters that are used here to supplement the original description of the family group and to accommodate a second genus, *Nemocataegis*, for which the radula and anatomy are unknown.

Three unique characters, in combination, were specified as diagnostic of the family group and genus (McLean and Quinn, 1987: 111–112): strong spiral cords, lack of columellar plications, and the oblique, broadly expanding aperture. Additional characteristic features include the deep, concave spiral interspaces lined with extremely fine prosocline or slightly sinuate axial threads and a dense microsculpture of discontinuous, reticulate or anastomosing, ridges and grooves that are infilled or overprinted by a chalky or crumbly brownish intritacalx (sensu D’Attilio and Radwin, 1971). The intritacalx may be so extensively developed as to obscure the microsculpture, but it clearly is not a continuous periostracal sheet. Intritacalx is also an important microstructural feature in two other seguenzioid families: Eucyclidae (Herbert, 2012) and Calliotropidae (see Hickman, 2016, for a discussion).

Macroscopic axial sculpture in *Cataegis* is restricted to elongate, fine nodules on the spiral cords. In all cataegids the columella is thickened, arcuate, lacking plications or teeth and covered with a thin callus that extends to cover the umbilicus completely or to leave a narrow umbilical chink. Interior nacre is not covered with a translucent inclined prismatic layer as in some seguenzioids, and it does not extend all the way to the growing margin of the shell, even in adults with descending sutures and final apertures. Spiral ornament is visible through the interior nacre as ridges and grooves. Fluting of the outer lip at the termination of spiral ridges and grooves is also characteristic of the family.

### Genus *Nemocataegis* new genus

**Type Species:** *Nemocataegis mcleani* new species.

**Description:** Shell small for family (height <15 mm), turbiniform, low spired, with rapidly expanding body whorl and large, oblique aperture; spiral ribs increasing by intercalation to >10 on body whorl and crossed by numerous thin, continuous, prosocline axial threads that form elongate nodes or sharp scales on spiral ribs; spiral grooves with microscopic sculpture and brownish intritacalx; columellar lip arcuate, smooth, and thickened by opaque callus; callus almost completely covering umbilicus as well as extending into interior margins of basal and apertural lips and covering nacre; adult suture and aperture descending; interior nacre with weak ridges and grooves reflecting exterior spiral sculpture.

**Remarks:** The new genus is clearly distinguished from *Cataegis* by its smaller shell size (<15 mm), more numerous, narrower, and prominently-beaded spiral cords, narrower spiral interspaces, lack of continuous periostracum, and well-developed intritacalx in microscopic grooves between crowded axial microsculptural threads.

It is unfortunate that the protoconchs are worn and that there are no data on the anatomy or radula. It is remarkable that the empty shells are so exquisitely preserved, and it is possible that the well-developed intritacalx has served a protective function against dissolution. Shells show no sign of encrustation, but there is evidence of repaired breakages. The known specimens come from gray mud at slope depths and are most likely deposit feeders.

**Etymology:** *Nemo* (Gr. thread) + *Cataegis*, in reference to the fine axial sculpture that distinguishes the threaded cataegids.

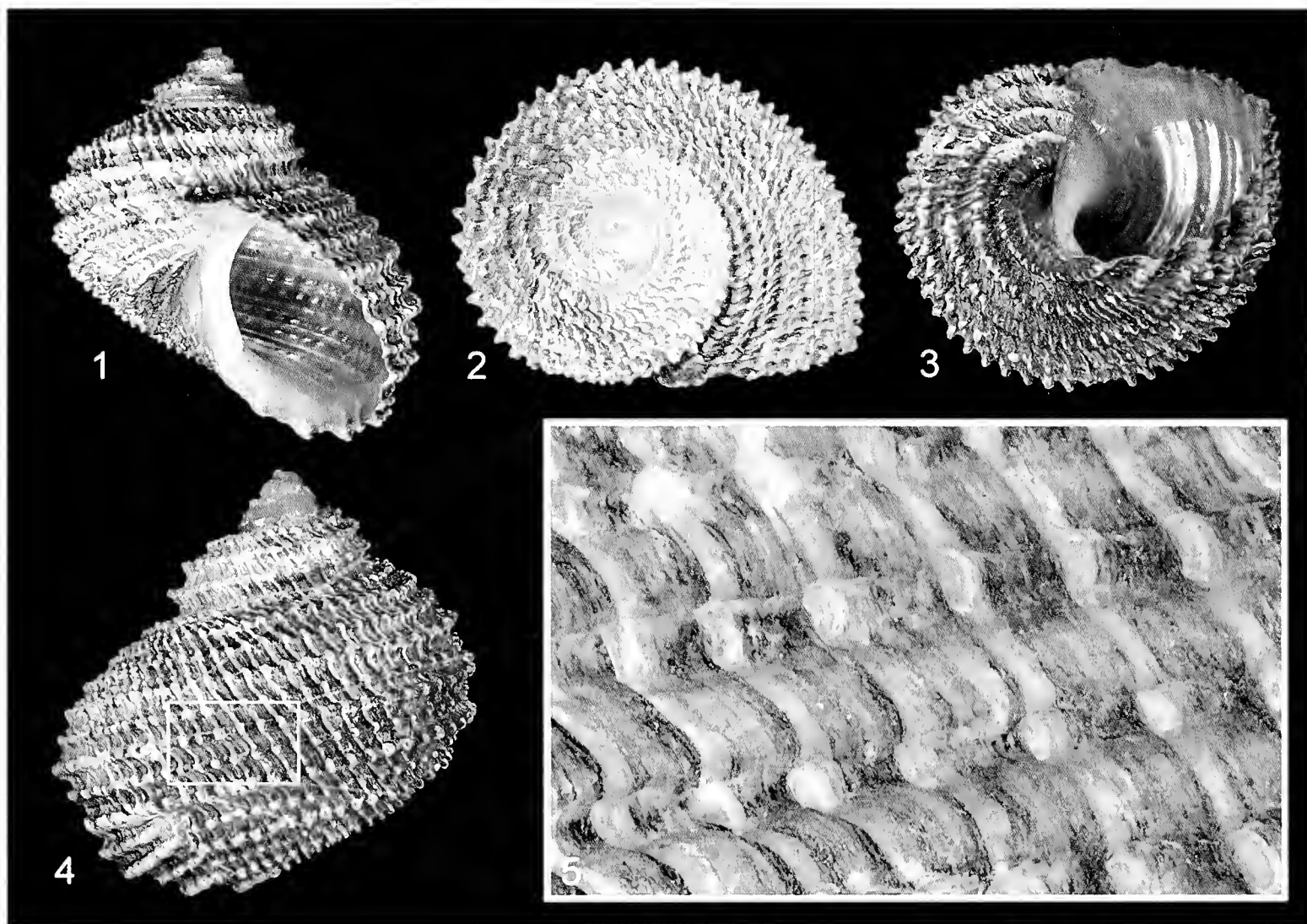
### *Nemocataegis mcleani* new species

(Figures 1–5)

**Diagnosis:** Enlarged body whorl evenly rounded, without peripheral or basal demarcation; 6 primary spiral cords visible in apical view, 5 additional spiral cords visible in umbilical view; secondary spiral cords intercalated between primary adapical spiral cords; axial ribs forming short, sharp, anteriorly directed spines on primary and secondary spiral ribs; thin callus deposit covering interior nacre on outer and basal lips overlapping columellar callus at base and top.

**Description:** The type species of *Nemocataegis* is clearly distinguished from *N. quinni* new species (described below) by more numerous primary spiral cords and more prominent, sharp, spinose projections where they are crossed by axial threads. The short spines are incompletely closed and project anteriorly (Figures 2, 3). In the deep spiral grooves the depressions between axial threads are filled with intritacalx that either obscures underlying structure or shows faint axial lineation (Figure 5).

**Holotype:** USNM 239464, height 14.4 mm, maximum width 14.0 mm.



**Figures 1–5.** *Nemocataegis mcleani* new species. 1. Semiapertural, 2. Apical, 3. Basal, and 4. Abapertural views of holotype, USNM 239464, height = 14.4 mm. 5. Detail from Figure 4 of nodose axial ribs and closely-spaced threads filled with brownish intritacalx.

**Type Locality:** 03°17'40" S, 120°36'45" E, Gulf of Boni (Bone), Celebese (Sulawesi), SE of Olang Point, 484 fathoms (=885 m), U.S. Fish Commission, R/V ALBATROSS, Station 5656, 19 December 1909, gray mud.

**Distribution:** Known only from the type locality.

**Etymology:** Named for the late James H. McLean in recognition of his many important contributions to understanding basal marine gastropods.

**Remarks:** The holotype appears to be an adult specimen on the basis of terminal growth features that include a descending suture and terminal translucent callus covering, but not totally obscuring, nacre inside the outer lip (Figure 3). Height and width are effectively equal. A major breakage in the basal portion of the outer lip (Figure 4) is repaired by a partially disjunct continuation of sculpture. The shell is remarkably fresh in appearance and was not encrusted by epizoans in the manner common to many calliotropids, especially those living on hard substrates.

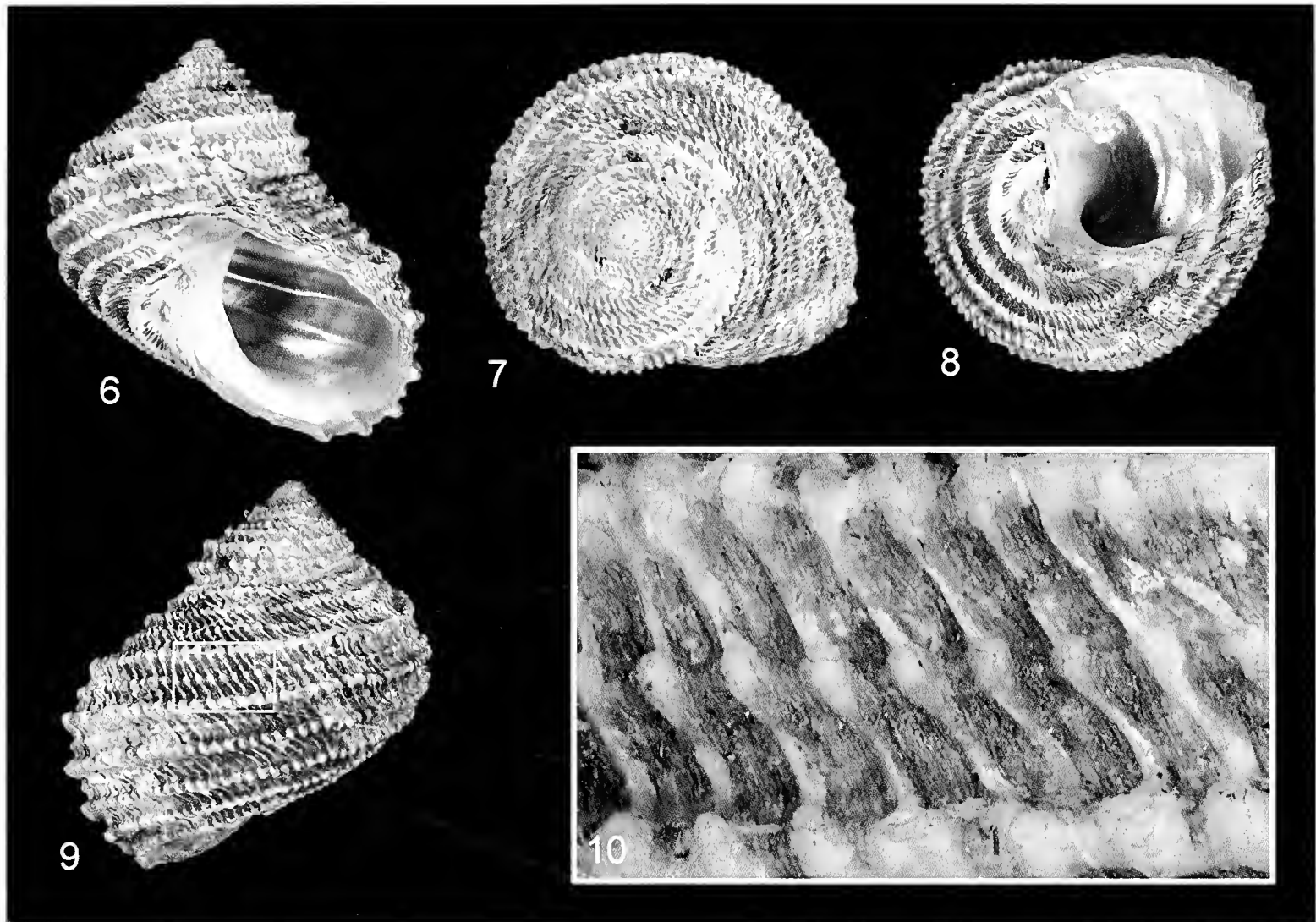
***Nemocataegis quinni* new species**  
(Figures 6–10)

**Description:** Enlarged body whorl with slightly concave shoulder slope; final aperture strongly oblique, with descending suture; spiral ribs of unequal strength and spacing, interspaces broader than ribs; numerous fine axial threads producing small blunt nodes at intersection with spiral ribs; brownish intritacalx well developed between axial threads in spiral interspaces; columellar callus reflected and covering umbilical region; columellar lip strongly arcuate, callus extending into aperture, partially obscuring interior nacre; interior nacre with weak spiral ridges.

**Holotype:** USNM 239279, Height 14.0 mm, maximum width 13.4 mm.

**Type Locality:** 00°19'20" N, 127°28'30" E, Molucca Sea, Halmahera, off Makian Island, 275 fathoms (=503 m), U.S. Fish Commission, R/V ALBATROSS, Station 5622, 29 November 1909, gray mud.

**Distribution:** Known only from the type locality.



**Figures 6–10.** *Nemocataegis quinni* new species. **6.** Semiapertural, **7.** Apical, **8.** Basal, and **9.** Abapertural views of holotype, USNM 239279, height = 14.0 mm. **10.** Detail from Figure 4 of nodose axial ribs and closely-spaced threads filled with brownish intritacal.

**Etymology:** Named for James F. Quinn, Jr. in recognition of his insightful contributions to the systematics of deep-sea gastropods.

**Remarks:** This species is distinguished from the type species by its more numerous, shorter and bluntly rounded nodes on the spiral ribs, a completely obscured umbilicus, slightly convex shoulder slope on the body whorl, more strongly descending final aperture, and less visible traces of spiral sculpture in the interior nacre. The terminal growth features on the shell of the holotype suggest that it is an adult. The brownish intritacal (Figure 10) is well developed in axial interspaces over the entire shell except at the apex. The protoconch small, but sufficiently worn that the boundary with the worn early teleoconch whorls cannot be discerned.

## DISCUSSION

In light of pronounced under-sampling of the deep-water fauna of Wallacean Indonesia, it is remarkable that the region contains so many species and higher taxa that have

never been recorded in relatively well-sampled regions of the Indo-Pacific. The endemic genus and two new species of Cataegidae described above join a diverse assemblage of basal gastropods that includes an endemic genus of Gazidae (Hickman, 2012) and six recently-described large-shelled species of Calliotropidae (Hickman, 2016).

Adequate sampling of the deep Wallacean fauna requires a protocol that recognizes factors that appear to be contributing the accumulation of relictual taxa. The primary purpose of this discussion is to extend previous characterization of deep Wallacea (Hickman, 2009a; 2009b; 2009c; 2012; 2016) and to provide a set of graphic illustrations (Figures 11–16) of the interacting components of deep Wallacean complexity.

This narrative begins with the currently known occurrences of species with deep (Paleozoic or Mesozoic) evolutionary origins and endemic or strongly disjunct representation in separate basins within Wallacea. It proceeds with components of explanation that are consistent with the objectives and tracks of previous collecting expeditions, the basins and sub-basins of Deep Wallacea, shallow oceanic circulation and path of the Indonesia Throughflow, the distribution of active volcanoes and

volcanic arcs, and the distribution of trenches, faults, and major tectonic features that are essential to understanding the geologic history of changing distribution of land and sea.

The term “Indonesian Archipelago” (the Malay Archipelago of Wallace, 1860; 1863; 1869) is a misnomer. A modern map Indonesia at the scale typically used to depict the islands of Oceania misses most of the more than 17000 islands and their arrangement. The region is actually a composite of separate archipelagic seas, straits and gulfs that have opened, expanded, contracted, and in some instances disappeared over a 200 My geologic history that began with the break-up of Gondwana (Metcalf, 2011). The larger islands in these seas have likewise moved, collided, fused, separated or disappeared during the tectonic evolution of the region. Many islands have emerged or submerged during its more recent eustatic history. The biogeographic effects of sea level change during the Pliocene and Pleistocene have received considerable attention from terrestrial and shallow marine biogeographers. Regional biogeography still lacks a deep marine perspective. Appreciation of the paleobathymetric complexity of the Wallacean seaways is, however, of increasing interest to physical oceanographers and meteorologists investigating large-scale influences of ocean circulation on global climate (e.g., Cane and Molnar, 2011).

#### ENDEMIC AND RELICTUAL TAXA IN WALLACEA

Occurrences of cataegid gastropods in deep Wallacea are illustrated in red in Figure 11, along with occurrences of calliotropid (green) and gazid (blue) vetigastropods, abyssochrysid gastropods (yellow), and a living coelacanth fish (star). Previous discussion (Hickman, 2016) of the deep geologic origins (Paleozoic or Mesozoic) and pronounced global disjunctions in these groups are consistent with the hypothesis that they are relictual taxa. The fossil records of more widespread geographic occurrence and greater taxonomic diversity are similarly indicative of a concentration of relictual taxa in Deep Wallacea.

#### EXPEDITIONS AND BENTHIC SAMPLING COVERAGE

Within Wallacea, the distributions shown in Figure 11 are correlated with the tracks of the Dutch SIBOGA Expedition of 1889–1900 and the R/V ALBATROSS Philippines Expedition of 1907–1910 (Figure 12). Although both expeditions produced remarkable oceanographic data, dredge samples, and new marine taxa from >200 meters, the research objectives were different in intent and execution as well as in their subsequent study and publication of results.

The SIBOGA Expedition was conducted under the leadership of Professor Max Weber, a distinguished zoologist at the University of Amsterdam, whose proposed track (shown in orange in Figure 12) was a zig-zag exploration of the margins of the region of deep marine basins between the Sunda and Sahul continental shelves.

His proposed track was not followed precisely, but it appears to reflect Weber’s curiosity about the terrestrial biogeographic lines that recently had been drawn by Wallace (1863) and Lydekker (1896) and their potential oceanographic correlates. The commander of the SIBOGA, G.F. Tydeman, was expert at recording deep soundings and oceanographic data (Tydeman, 1903) from the >300 sampling stations. Most remarkably, the taxonomic results were published in a series of >100 monographs and included descriptions of the prosobranch gastropods (Schepman 1908; 1909). For a summary of the SIBOGA and other Dutch Oceanographic research in Indonesia in colonial times, see Van Aken (2005). The specimens were from both shallow and deep stations on the periphery of the region, and the SIBOGA did not sample in the gulfs, basins, and sub-basins of Sulawesi and Halmahera.

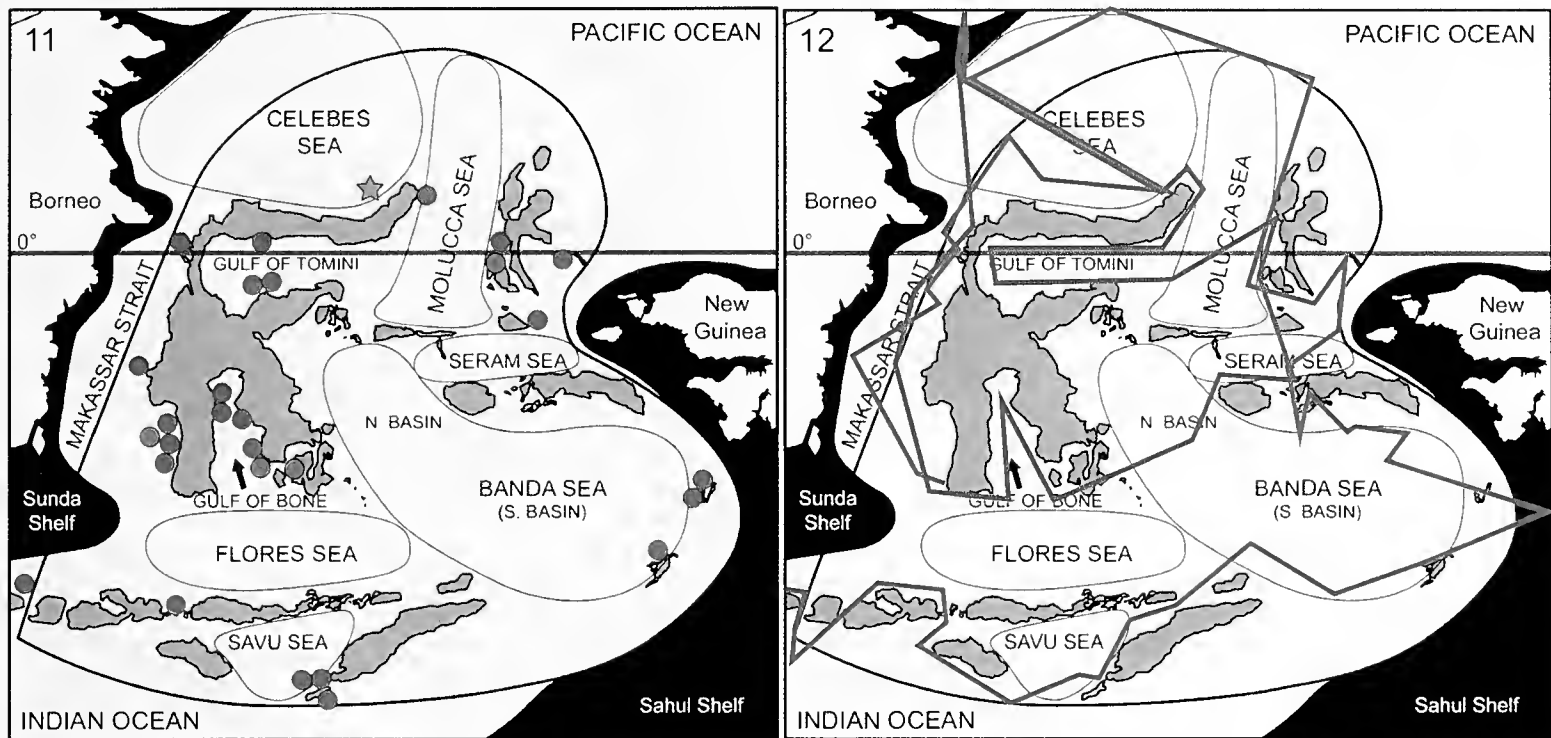
The ALBATROSS Philippines Expedition was designed as a focused survey of the aquatic resources of the Philippine Islands, under the command of Hugh McCormick Smith of the U.S. Bureau of Fisheries. It was conducted as a series of cruises, with the addition of a final two months in the Dutch East Indies (Indonesia) at the end. The major biological reports are on the fishes (see Smith and Williams, 1999). The track of the ALBATROSS in Indonesia is shown in purple in Figure 12).

Little is known about the objectives or why the cruise was narrowly focused on obtaining collections and data from deep stations in Sulawesi (Makassar Strait, Gulf of Bone, and Gulf of Tomini) and the western margin of Halmahera. Malacologist Paul Bartsch, who had represented the Smithsonian Institution in the preceding Philippines cruises, left the expedition before it departed for Indonesia. Hugh McCormick Smith also had departed, and there is no record of who was in charge. What little we do know is from the autobiography of Roy Chapman Andrews, who was recruited as a 24-year-old graduate student and charged with terrestrial collecting. He notes (Andrews, 1943: 67) that “It wasn’t a ‘happy ship’” and that he was “supposed to have no part in the dredging operations” (p. 72). He makes no mention of marine mollusks in his romanticized account.

In spite of what little is known samples were obtained from 72 stations between 7 November and 30 December 1909. Specimens and station data were meticulously processed and accessioned into the Smithsonian mollusk collection and archives and are still being discovered and studied by malacologists with expertise in various taxonomic groups.

With the exception of the SIBOGA Expedition and its monumental series of reports, oceanographic research during colonial rule in Indonesia has been characterized as a “gunboat science” (Van Aken, 2005). However, Van Aken’s (2005) summary highlights many important hydrographic, physical and chemical oceanographic, and geophysical data that were obtained and published by dedicated scientists who obtained private funding.

A limited biological sampling effort in 1922 in the vicinity of Kai and Tanimbar was aimed at evaluating a proposed Danish tropical marine station (Mortensen,



**Figures 11–12.** Simplified maps of marine Wallacea comparing occurrences of relictual deep-water taxa and tracks of major collecting expeditions. **11.** Collecting sites for cataegid (red circles), calliotropid (green circles), gazid (blue circle) and abyssochrisid (yellow circles) gastropods; and living fossil coelacanth fish (blue star). **12.** Tracks of the *Siboga* Expedition (orange) on the margins of Wallacea and the *Albatross* Expedition (purple) within northwestern Wallacea.

1923) and contributed no deep-water gastropods pertinent to this discussion. The KARUBAR joint Indonesian and French cruise in this region, also sampled primarily at shallower depths (< 500 m) with a strong focus on the Arafura Sea (outside of Wallacea) rather than in the Banda Sea (Crosnier et al., 1997). An additional joint Indonesian and French sampling effort (CORINDON 2) (Moosa, 1984) sampled deep-water stations on either side of the Makassar Strait, adding a abyssochrisid records, including a new species (Bouchet, 1991).

#### BIOGEOGRAPHIC LINES AND THE EVOLVING CONCEPT OF WALLACEA

More than enough has been written about the drawing of lines by terrestrial biogeographers in the Indonesian region (e.g., Mayr, 1944; Michaux, 2010). From a marine perspective, the margin of the Sunda Shelf to the west and margin of the Sahul shelf to the east define Wallacea as a region in precisely the manner originally intended by Dickerson (1924) when he proposed the term. Wallacea is illustrated here (Figure 13) as lying between the “Wallace Line and Weber Line slightly modified” (see Dickerson, 1924: fig. 1).

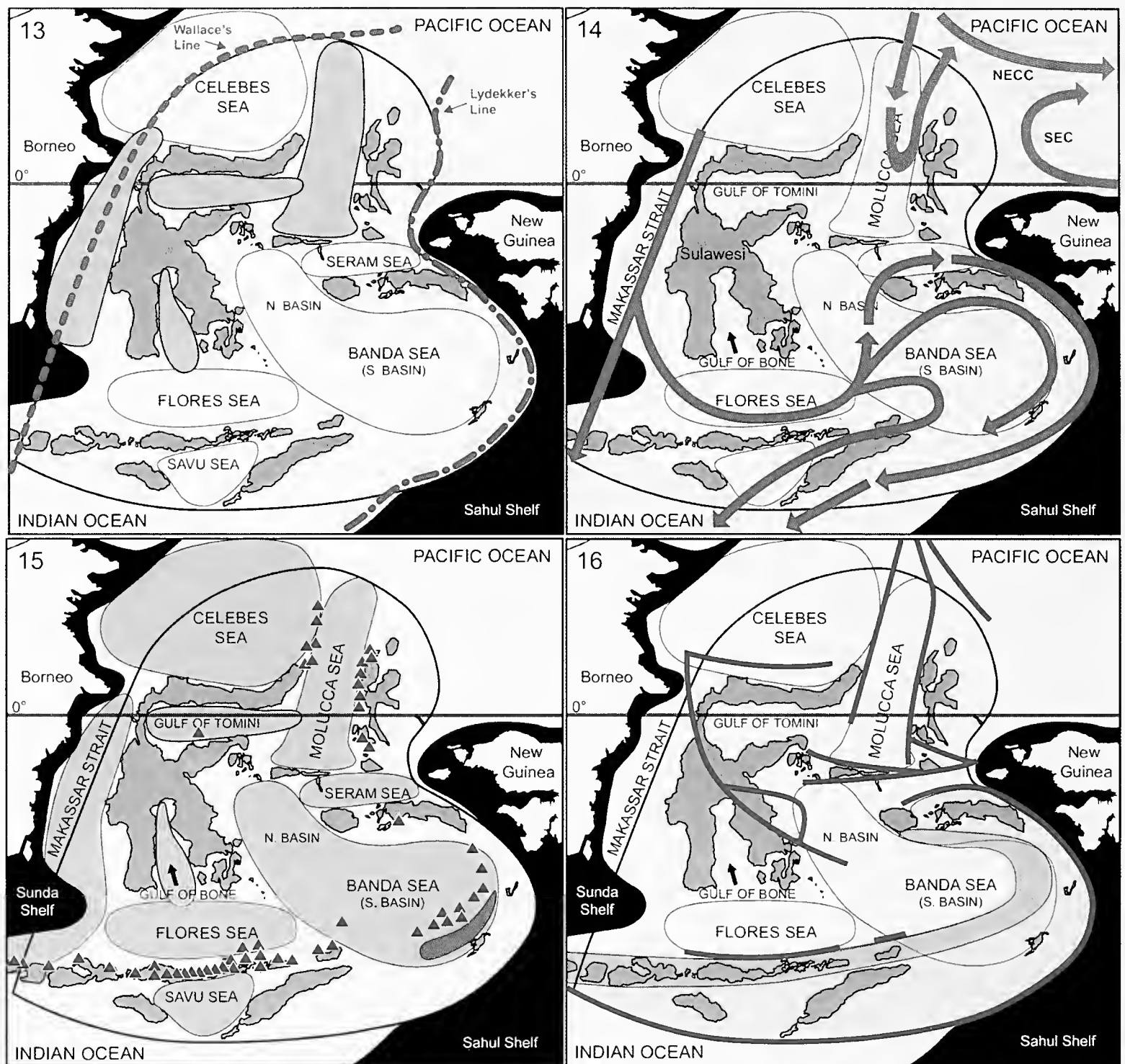
The Oceanographic Data Set for the ALBATROSS sampling in Indonesia includes 71 stations concentrated close to shore in four separate basins adjacent to Sulawesi and Halmahera (Makassar Strait, Gulf of Bone, Gulf of Tomini, and Molucca sea). These basins are shown in blue (Figure 13). In each setting, the 200 m isobath is very close to shore, and 56 of the stations sampled were from depths >200 m, 30 stations were from >1,000 m and 13 stations were from >1,500 m.

Restriction of marine fauna to individual basins, gulfs, and straits within Wallacea is consonant with the complex geological history of fragmentation and amalgamation in marine Wallacea as a whole. Similar recognition of multiple sub-regions of endemism in the terrestrial biota (e.g., Michaux, 2010) advances biogeographic analysis as an integration of distributional data with geotectonic history.

#### THE INDONESIAN THROUGHFLOW AND SHALLOW OCEANIC CIRCULATION

Patterns of distribution of marine invertebrates in Wallacea are typically examined in terms of the oceanic currents that transport and disperse pelagic larvae. Considerable emphasis has been placed on the potential importance of the Indonesian Throughflow (ITF) in determining patterns of genetic connectivity. The gateway connection between the North Pacific and the Indian Ocean (Figure 14) is a complex system of shallow and deep currents. The main route is a shallow southward flow of the Mindanao Current through the Celebes Sea and Makassar Strait. It enters the Indian Ocean between Bali and Lombok with another branch turning eastward through the Flores Sea, branching again to flow through the Banda Sea, entering the Indian Ocean through the Ombai Strait and Timor Passage on either side of Timor.

Minor secondary flow through the Molucca Sea and into the Banda Sea is more complicated. North Pacific water is initially deflected from reaching the Banda Sea by eastward reversal of flow in the South Equatorial Current (SEC) into the North Equatorial Counter Current



**Figures 13–16.** Simplified maps of factors correlated with occurrences of relictual deep-water taxa. **13.** Outline of Wallacea bounded on the west by Wallace's Line (purple dashes) and the east by Lydekker's Line (broken purple dashes), and the four deep basins (blue) from which the *Albatross* gastropod specimens were dredged: Molucca Sea, Gulf of Bone, Makassar Strait, and Gulf of Tomini. **14.** Surface currents of the Indonesian Throughflow (ITF) from the North Pacific through the Southeast Asian Gateway to the Indian Ocean and surface currents with no significant flow through Wallacea (gray). **15.** Nine major Wallacean basins underlain by oceanic lithosphere (blue), the anomalously deep Weber Basin (deep blue), and historically active volcanoes (red triangles) defining basin boundaries. **16.** Fault systems and subduction zones (red) associated with major tectonic terranes, and position of the outer (light pink) and inner (dark pink) zones of the Banda Arc.

(NECC) influenced by several large semi-permanent eddies (Arruda and Nof, 2003). Deeper flow entering the Banda Sea is further impeded by sills and physical barriers separating sub-basins (Gordon et al., 2003; Van Aken et al., 2009). The Banda Sea appears to contribute a relatively minor amount to total throughflow (Gordon and Fine, 1996). This is an oversimplification of

a temporally and spatially variable pattern that is incompletely characterized in spite of a growing body of detailed oceanographic data. The patterns of flow vary on time scales ranging from days and seasons to decades and significant periods of geologic time (Tillinger, 2011).

While the ITF (shown in Purple in Figure 14) and interactions with the boundary between major gyres and

eddies (shown in gray in Figure 14) may be significant factors in the dispersal and connectivity in the hyper-diverse shallow marine biota of Wallacea, they are less likely to play a role in understanding the endemism in deep-water caudofoveate, caudofoveate, or caudofoveate gastropods (Hickman, 2012, 2016). From an oceanographic perspective, this is because deep-water current systems are different and from a biological perspective because deep-water vetigastropods lack a significant pelagic dispersal stage in their life history. They likewise have been unaffected by Pliocene and Pleistocene sea-level change and because they occur in basins that are isolated from one another by submarine topographic barriers that restrict the dispersal of benthic adults.

#### MARINE BASINS AND VOLCANIC ARCS

There are at least 26 bathymetrically distinct basins within the Wallacean region that reach bathyal depths (>200 m). The nine illustrated in blue (Figure 15) contain species of basal marine gastropods in clades associated with chemical energy sources. The Wallacean basins are alternatively identified in the literature and on maps as seas (*laut*), straits (*selat*), or gulfs (*teluk*). Straits are narrow passages between islands, while gulfs are deep inlets or indentations in the larger emergent landmasses, notably the Gulf of Tomini and the Gulf of Bone in Sulawesi. Complex ridge systems create bathymetric isolates in some of the basins. Examples in the Banda Sea include a main North Basin (Sula) and a South Basin that is further subdivided into the Wetar, Damar, and Weber basins. The Weber Deep (in dark blue) is an anomalous, tectonically generated bathymetric isolate in the Banda Forearc with depths exceeding 7 km. The Makassar Strait, the Bone Basin, and the Gulf of Tomini also contain bathymetrically distinct sub-basins. Although bathymetry and submarine topography can confine or restrict benthic taxa that lack a planktonic dispersal phase, bathymetric complexity must be further integrated with the geologic history. This is especially true of volcanic arc activity that has shaped basin development and the sedimentary component of deep-water ecosystems.

The link between geologic and ecologic settings in deep Wallacea has not been explored. Understanding the role of volcanic arcs in basin development, sedimentation, underlying stratigraphy, structure, geophysics, and geochemical peculiarities is crucial to understanding the deep benthic realm in which endemic and relictual taxa have accumulated. The major abiotic features of magmatic arc history (Hall and Smyth, 2008) provide a framework and starting point for future integrative study.

The modern volcanic arcs in Wallacea (Figure 15) are depicted by red circles representing volcanoes that have been active historically (Smithsonian, 2016). There are many more named volcanic edifices that are presumably inactive, and little is known of submarine volcanism.

The subduction zone system in Wallacea includes four volcanic arcs (Figure 15). The Sunda and Banda volcanic chains mark the zone of melting as the Indo-Australian

plate is subducted beneath the Eurasian Plate. To the north, the Sangihe (or North Sulawesi Arc) and the Halmahera Arc mark the convergent margins of the formerly larger Molucca Sea Plate that is disappearing in a unique modern example of double subduction system. The constriction of the formerly broad Molucca Seaway necessarily represents a constriction of deep marine habitat and is consistent with the occurrence of relictual molluscan taxa (Hickman, 2012; 2016).

Much of the basin formation in Wallacea appears to be driven by extensional rather than compressional tectonic forces (Charlton, 1991; Charlton et al., 1991; Hall, 2013; Pownall et al., 2013). These include the opening of both of the two deep interarm basins of Sulawesi: the Gorontalo basin in the Gulf of Tomini (Pholbud et al. 2012) and the Bone Basin in Sulawesi (Sudarmono, 2000). The importance of slab rollback and lithospheric extension in the Banda Arc is perhaps most dramatic in the proposed detachment model for formation of the Weber Deep (Pownall et al. 2016).

Further understanding of basin history requires examination of subsurface structure, which is difficult to depict and interpret in simplified map view. The following section highlights some of the Wallacean structural features that are especially germane to the peculiar geographic distribution of deep-water marine gastropods.

#### MAJOR STRUCTURAL FEATURES AND HISTORY

The major structural features of Wallacea (Figure 16) provide a starting point for understanding the complex history that is treated in a diffuse and evolving body of literature and lively debate over alternative interpretations (See Hall, 2011; 2013; Hall and Blundell, 1996; Hall and Wilson, 2000; Hall et al. 2011 and references therein). Full understanding of modern Wallacea requires going back to the Paleozoic break-up of greater Gondwanaland and tracing separation and movement of micro-continental fragments, the openings new ocean basins, the collision and suturing of slivers, translations and subductions, and disappearance of some of the features ultimately responsible for the modern distribution of tectonically bounded marine basins and terrestrial blocks and fragments (e.g., Metcalfe, 2001; 2011). Features depicted in red in Figure 16 include active trenches, major sutures, thrust faults, and strike-slip faults and fault zones.

The most prominent structural feature is the horseshoe-shaped Banda Arc (Figure 16), a complex suture zone in which multiple Jurassic to Neogene pre-collisional imbricate wedges are continuous with post-collisional evolution of the modern forearc (Charlton et al., 1991). The zones of folding and thrusting of the outer arc are complex (successively older from southeast to northwest) and the modern deep forearc basin are represented in pink, in Figure 16). The Islands and volcanoes of the active inner arc are represented in salmon. The Banda Arc is an exemplar of an arc-continent collision with multiple episodes of accretion of crustal blocks and fragments and is treated in an extensive

literature (e.g. Bowin et al., 1980; Charlton et al, 1991; Hall and Wilson, 2000; Harris, 2006; and references therein).

Three additional suture zones (Figure 16) are: (1) the Sulawesi Suture, also a complex region of multiple collisions, (2) the Sorong Suture, a major east-west trending fault zone of multiple collisions, and (3) the Molucca Suture where two colliding volcanic arcs are converging to close the ancient Molucca Seaway (see Hall and Wilson, 2000 for a review and references).

The relevance of the Wallacean suture zones to marine biogeography, endemism, and the deep-water relictual gastropod taxa resides in the clear evidence of geochemically unusual and extreme environments of interest to petroleum geologists, who have identified commercial hydrocarbon occurrences (Charlton, 2004), hydrocarbon seeps (Camplin and Hall, 2014) and mapped fields of mud volcanoes (Barber et al., 1986).

Biological expedition reports provide few clues to geochemical and sedimentary settings at sampling stations. However, the increasing geological evidence in deep Wallacea for both explosive and diffuse expulsion of fluids rich in sulfides and hydrocarbons (Hickman, 2016) are consonant with the presence of (1) taxa that have been identified elsewhere in the world as part of chemosynthetically based communities, (2) adaptations to toxic fluids and hypoxia, and (3) nutrition based on elevated productivity of chemosynthetic microbes and microbial mats.

## CONCLUSIONS

Understanding of the marine biogeography of Deep Wallacea is in its infancy. Distribution of relictual basal gastropod taxa is linked to features mapped in this paper: expedition tracks and biological sampling, positions of discrete marine basins and their topographic boundaries, patterns of ocean currents and circulation, distribution of active volcanoes and volcanic arcs, and distribution of what remains of the complex structural record of tectonism over many millions of years. A full geobiological history will emerge only through integrating data from the disparate sources and disciplines implicated above. At the same time, interdisciplinary exchange is likely to assist both geologists and biologists in addressing separate, discipline-specific questions. It is ironic that a paleontologist should find herself attempting to unravel a deep-water geobiological history that has no preserved fossil record in Wallacea. However, it is those with formal training in both geology and biology who are most likely to be challenged and attracted to this kind of integrative effort.

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# A revision of the Hispaniolan genera *Chondropomella*, *Chondropomium*, and *Clydonopoma* (Gastropoda: Annulariidae), with the recognition of a new genus, *Superbipoma*: phylogenetic, radular, and conchological evidence

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## ABSTRACT

The annulariid genera *Chondropomella*, *Chondropomium*, and *Clydonopoma* are believed to have originated from the Tiburon/Barahona Peninsula in isolation from the rest of Hispaniola. *Chondropomium* has colonized the rift valley and adjacent river valleys between the Tiburon Peninsula and the remainder of Hispaniola. It is primarily limited to xeric lowlands, rarely found above 200 m elevation. Little is known about the rare *Chondropomella* but they seem to occur in the rift valley in xeric areas as well. In contrast, *Clydonopoma* is endemic to the Sierra Baoruco with a single species in the adjacent eastern Massif de la Selle and occupies the upland mesic forests and pine savannahs between 200–4000 m. The most widely distributed species, *Chondropomium weinlandi*, has been the subject of considerable confusion concerning the nature of its many color forms or subspecies, as well as its valid name. This species was investigated using phylogenetic methods and compared to congeners and related genera. A phylogenetic study aimed at elucidating relationships among these taxa analyzed a partitioned matrix of nuclear (ITS 1) and mitochondrial (CO1, 12S, 16S) DNA sequences in a Maximum-likelihood framework under the GTR+I substitution model. Contrary to Bartsch's 1946 assessment that *C. weinlandi* is a complex of subspecies, it is here shown to be a single, highly polymorphic species for color. The new genus *Superbipoma* is recognized based on phylogenetic, radular, and conchological evidence. It contains two species: *S. asymmetricum* (Henderson and Simpson, 1902) and *S. superbium* (Pilsbry, 1933). Eleven species of *Chondropomium* are recognized including two new species: *C. caelicum* and *C. sardonys*; three species of *Chondropomella* and nine species of *Clydonopoma*, including one new species, *Clydonopoma titatum*, are recognized. A calcified operculum is the ancestral condition for the Annulariidae. In *Clydonopoma* and *Chondropomella* the operculum is a particularly complex calcified structure termed the pseudolamella. This structure has been lost in *Chondropomium* and *Superbipoma*.

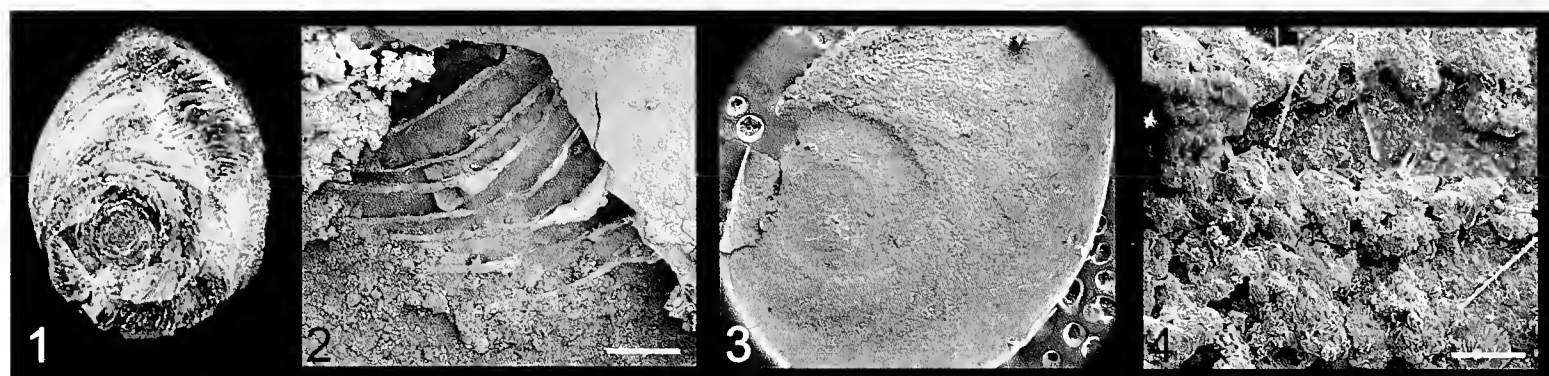
*Additional Keywords:* Haiti, Dominican Republic, land snail, DNA sequence, molecular systematics.

## INTRODUCTION

Hispaniola consists of two historically separate geological entities, the Tiburon Peninsula and the remainder of Hispaniola. The Tiburon Peninsula (termed the Barahona Peninsula in the Dominican Republic) was an isolated island on the Caribbean Plate before beginning its ongoing collision with Hispaniola in the Pliocene (Miller and Miller, 2001). The intervening space between the two land masses is now the rift valley of Hoya de Enriquillo in the Dominican Republic and the Plain du Cul-de-Sac in Haiti. This includes several lakes that may represent the last vestiges of ocean between them: Lago Enriquillo, Lago del Rincón, and Étang Saumâtre.

The Annulariidae are widely distributed across both of these parts of Hispaniola. However, phylogenetic evidence (Skomrock, 2014) suggested that the faunas of the two regions remained distinct, reflecting the ancient isolation of the two parts and the highly endemic nature of most species. The four genera reviewed here are part of the Tiburon fauna and many are limited to narrow ranges of the Sierra Baoruco on the Barahona Peninsula. The species are overall quite similar to each other and the genera were loosely defined by shell and opercular characteristics. The phylogenetic relationships between the taxa were unknown. In particular, several taxa display high degrees of shell color variation that have been described as subspecies by some authors. Recent collections indicate that these populations are sympatric and cannot be subspecies, but the question remained as to their relationships to each other.

Like all annulariids, these species are calciphiles, never found far from a limestone source. They commonly occur in association with limestone knolls, mogotes, fossilized reefs, and karst topography, which are common in the Tiburon area. Because of their dependency on limestone many species are highly



**Figures 1–4.** Opercula. **1.** *Clydonopoma peasei* (Pilsbry, 1933). Pseudolamellate operculum showing pseudolamella partially broken away from underlying support, 7 mm length. **2.** *Clydonopoma poloense* (Bartsch, 1946). Pseudolamella at edge supported by erect calcified ribs on corneous base. Scale bar = 400  $\mu\text{m}$ . **3, 4.** *Chondropomum marmoreum* (Watters and Duffy, 2010). **3.** Operculum with calcareous deposit on outer surface, 5 mm length. **4.** Calcareous deposit on outer surface. Scale bar = 100  $\mu\text{m}$ , crystals at bottom of micrograph are an artifact of fixation.

endemic, with outcrops acting as islands of speciation among more inhospitable intervening areas. To the north in central Hispaniola is the Cordillera Central, which is predominately granitic and largely devoid of annulariids. But even there, species will be found in calcareous areas where available.

Members of the four genera reviewed here are unusual in several respects. They are large for the family (to ca. 35 mm in length) and have a shell sculpture consisting of (usually) only polished axial ribs. This sculpture seems adapted for a burrowing lifestyle beneath rocks and plants, offering little resistance in the burrowing direction. *Clydonopoma* and *Chondropomella* have a highly specialized type of operculum termed a pseudolamella (Figures 1, 2). As in all annulariids, the operculum is attached to the foot as a thin, corneous layer. In *Clydonopoma* and *Chondropomella*, the operculum is paucispiral, with closely-set, erect calcified ribs arranged in a pin-wheel fashion on top of the corneous layer. The distal edges of these ribs are fused to form a second calcified surface parallel to the corneous base termed the pseudolamella. In contrast, the operculum of *Chondropomium* and *Superbipoma* lacks a pseudolamella and consists only of the corneous plate, although often overlain with a layer of microscopic, calcified crystals (Figures 3, 4). The genus *Crosseopoma* (not reviewed here) also has a pseudolamella, but in that genus there is a sulcus separating the opercular whorls; the lip is also single in *Crosseopoma* rather than double as in *Clydonopoma* and *Chondropomella*.

This study reviewed these groups using phylogenetic, radular, and conchological evidence. Although the family as a whole was phylogenetically studied by Skomrock (2014), this review looked at a much finer scale to discern the relationships not only of genera and species, but individual populations.

Abbreviations and text conventions are: {}: Used by Thiele (1929) for the category Tribe; ANSP, Academy of Natural Sciences, Philadelphia, USA; BSM: Bailey-Matthews National Shell Museum, Sanibel, USA; CMNH, Carnegie Museum of Natural History, Pittsburgh, USA;

MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; GTW, Collection of the author, Columbus, USA; NHMUK, Natural History Museum, London, UK; USNM, National Museum of Natural History, Washington, USA; OSUM, Ohio State University Museum of Biological Diversity, Columbus, USA; UF, Florida Museum of Natural History, Gainesville, USA; ZMB, Zoologisches Museum Berlin, Federal Republic of Germany.

## MATERIALS AND METHODS

**Molecular Data Collection:** Of the 24 taxa reviewed here, suitable genetic material was only available for 25 specimens of seven species (Table 1). Most species have either never been collected alive or if so, inadequately preserved. The sympatric *Crosseopoma vermiculatum* (Bartsch, 1946) is conchologically very similar to *Chondropomium* and, although the genus was not reviewed here, was included in the phylogenetic analysis as a possible misplaced member of *Chondropomium*. A species of *Abbottella*, now placed in its own subfamily (Abbottellinae) within the Annulariidae (Watters, 2016b), was included as well. Members of the sister family Pomatiidae were included as the outgroup.

DNA was extracted from foot tissues of preserved specimens representing species from Pomatiidae (outgroup) and Annulariidae (ingroup) using the DNeasy (Qiagen Hiden, Germany) blood and tissue kit according to the rodent tail protocol. Nuclear (ITS 1) and mitochondrial gene regions (CO1, 12S, 16S) were amplified using new and previously published primers. Custom degenerate primers were developed for 12S based on those reported for Mollusca by Machida et al. (2012) as follows: 12S forward primer sequence 5'-GTGCCAG-CADYYGCGGTYA-3'; reverse primer sequence 5'-AGRGYGACGGCGCATDTGW-3'. Partial Cytochrome Oxidase subunit 1 was amplified using universal primers LCO1490, HCO2198 (Folmer et al., 1994); 16S and ITS 1 were amplified with the mollusc-specific primers published by Pfenninger et al. (2005).

Multiple-band PCR results occurred for ITS and 12S in some but not all individuals. In these cases, the band matching the length of single-band results in other specimens (~600bp for 12S, ~300bp for ITS) was extracted via Qiaquick gel extraction kit (Qiagen). Extracted DNA was then subjected to a second round of PCR and gel electrophoresis. PCR products were sequenced by GeneWiz (South Plainfield, New Jersey). All DNA sequences were searched against the NCBI nucleotide database using the BLAST (Altschul et al., 1990). Any sequence with the top BLAST result not matching a gastropod was excluded from the analysis.

**Phylogenetic Analysis:** Trimmed sequences for each locus were aligned by MUSCLE (Edgar, 2004) implemented through Geneious v.7.1.9 (Biomatters) and using default parameters. A complete data matrix was tested for an optimal partitioning scheme and a nucleotide substitution model in PartitionFinder (Lanfear et al., 2012) under the AICc. Possible partitions were defined as each individual locus plus three codon positions of CO1, resulting in a maximum of six possible partitions. Using the OSU Ohio Biodiversity Conservation Partnership computing cluster, the sequence matrix was analyzed in RAXML v. S.1.16 (Stamatakis, 2014). Twenty independent runs were followed by 10,000 bootstrap replicates on the best scoring tree to assess clade support. Each sequenced gene region was also analyzed independently in the same manner as the complete data matrix. A second analysis of the complete matrix was carried out in MrBayes v. 3.2.6 (Ronquist and Huelsenbeck, 2003). The Bayesian analysis was also run on the full, partitioned data set using the GTR+ $\Gamma$  model for two million generations with 500,000 discarded as burn-in. Prior distributions were left as defaults and trees were sampled every 500 generations.

**Radulae:** Radulae were available for eight of the taxa. Radulae were removed from ETOH preserved specimens and placed in commercial bleach until all attached tissue had been dissolved (typically 10–15 minutes). The remaining radular ribbon was washed in two changes of 100% ETOH and placed on an SEM stub. Specimens were sputter-coated with gold-palladium and viewed with a Philips XL30 scanning electron microscope at an accelerating voltage of 20 KeV.

More than 4000 shells were examined. Descriptions and measurements were based on shells oriented with the spire up and the aperture facing the viewer. Measurements are for adult shells unless noted otherwise. Length was measured from the tip of the protoconch (or teleoconch of decollate specimens) to the opposite anteriormost extension of the outer lip. Subsets of the largest and smallest adult specimens were selected by eye from all available specimens and measured to determine the minimum and maximum lengths. The number of whorls was determined using the 1 D method of Van Osselaer (1999).

Original descriptions from non-English sources are translated and given with each species review. Specimens used in the phylogenetic portion are highlighted in bold

text in the “Other Material Examined” section of each species. Numbers in parentheses after catalog numbers are the number of specimens in the lot.

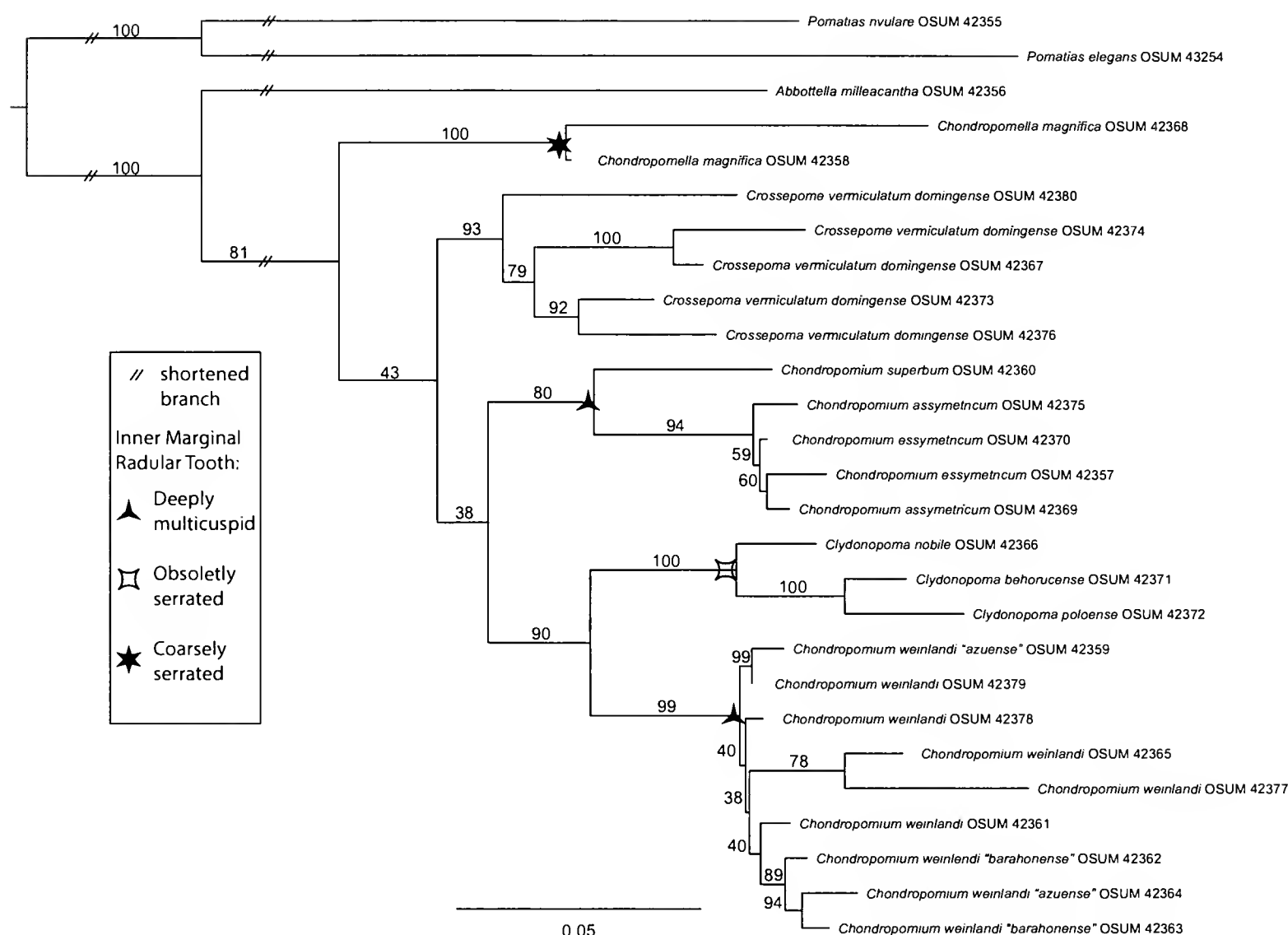
## RESULTS

Sequences for two or more loci were obtained for 25 specimens. All sequences used in the analysis have been submitted to GenBank (see Table 1 for accession numbers). The complete data set was an aligned, concatenated matrix of 2369 nucleotides in length. The optimal scheme identified by PartitionFinder included all six separate partitions and GTR+ $\Gamma$  as the favored partition scheme and substitution model, respectively.

All 20 ML replicate runs of the full data set produced an identical tree topology. Bootstrap support was generally high at the genus level (supporting generic monophyly) but poor at intermediate nodes. All subspecies (morphotypes) or putative species of *Chondropomium weinlandi* formed a single monophyletic clade, but morphotypes within the group did not segregate. We recovered high support for a sister relationship between individuals of different types to the exclusion of their comorphs (e.g., 94% bootstrap support for *C. weinlandi* “azuense” and *C. weinlandi* “barahonense” and 99% for another *C. weinlandi* “azuense” with *C. weinlandi*) (Figure 5). This result is consistent with a single diverse species rather than subspecific radiations.

The topology of all four ML single-gene trees differed from each other with respect to genus-level relationships, but in most cases the putative genera (*Crossepoma*, *Chydonopoma*, *Chondropomium*, and *Superbipoma* new genus) are recovered as monophyletic groups. Exceptions are that in the 12S gene tree, two individuals of *Chondropomium* nest within a poorly supported (21% bootstrap) *Crossepoma* clade, while *Chydonopoma* species are distributed among *Superbipoma* and *Chondropomium* species (20% bootstrap), and in the CO1 gene tree, *Superbipoma* new genus is recovered as a paraphyletic grade at the base of the ingroup. As in the combined analysis, putative species in the *Chondropomium weinlandi* clade fail to segregate based on shell morphology regardless of the gene region analyzed. Only in the ITS gene tree do individuals of *Chondropomium superbium* and *Chondropomium asymmetricum* (= *Superbipoma* new genus) form a weakly supported sister-relationship with *Chondropomium weinlandi*. All other genes support a *Chydonopoma*-*Chondropomium weinlandi* sister-relationship (CO1, 16S) or a *Chydonopoma*-*Superbipoma* sister-relationship (12S). The Bayesian analysis was ended after two million runs with a final average standard deviation of split frequencies of 0.006. The pertinent results of the Bayesian analysis agree with those of the ML analysis, with a strongly supported (100% posterior probability) relationship between the *Chondropomium weinlandi* and *Chydonopoma* clades and species of *Chondropomium weinlandi* failing to segregate by morphotype.

Reconstruction of ancestral characters suggest that calcification of the operculum and the presence of



**Figure 5.** Inferred relationships from maximum likelihood analysis of DNA sequence data. Symbols at the base of clades mark the condition of the inner marginal radular tooth for all terminals in that clade. Bootstrap support values appear above or left of branches. Bar represents branch length at which 0.05 substitutions per nucleotide site have occurred.

a pseudolamella are both ancestrally present in the taxa of Annulariidae reviewed here (pseudolamella does not occur in *Abbottella*). Two subsequent losses of the pseudolamella in *Superbipoma* and *Chondropomium* (proportional likelihood of 0.81 and 0.79, respectively, for "presence" in nodes immediately preceding the 'loss' bars in Figure 5) are inferred. While the calcification of the operculum has been reconstructed as possibly a loss with subsequent gain in *Clydonopoma*, it is more likely that the pseudolamella persisted in that genus. The conchologically similar *Crosseopoma vermiculatum*, which possesses a pseudolamella, included as potentially a *Chondropomium*, is shown to belong to a genus apart from those reviewed here.

Radulae delineated the same genera as identified here by phylogenetic and conchological characteristics. The inner marginal was the most variable between taxa and of the most systematic importance. The remaining radular teeth showed remarkable uniformity, with some exceptions. A more extensive study of the radulae of 111 annulariid species found similar results (Watters, in prep.). In that study, as here, *Abbottella* (and related genera) differed in radular characteristics from most

other annulariids. *Abbottella* was raised to subfamily rank within the Annulariidae by Watters (2016b).

## SYSTEMATICS

Family Annulariidae Henderson and Bartsch, 1920

### Genus *Chondropomium* Henderson and Bartsch, 1920

**Type Species:** *Chondropoma weinlandi* Pfeiffer, 1862, by original designation.

**Description:** Shells medium to large for family (to ca. 25 mm length), elongate-conic, usually decollate. Protoconch of 1.5 smooth, minute whorls. Final whorl shortly detached from previous whorl. Axial sculpture of wide, flattened, close-set ribs. Spiral sculpture absent on final whorl but present in umbilicus; rarely on earlier whorls. Overall sculpture very smooth, often polished. Suture minutely serrate lacking fused tufts. Adult with very narrowly reflected lip. Lip single or double; when double,

inner lip usually fused to outer lip. Color pattern of bands and blotches, continuous or interrupted; rarely lacking any pattern. Operculum paucispiral, with uniform, thin granular deposit. Taenioglossate radula with rachidian tooth, single pair of lateral teeth, and two pairs of marginal teeth. Rachidian and lateral teeth usually unicuspid. Inner marginal tooth deeply multicuspid on outer side. Outer marginal tooth pectinate. Animal with foot longitudinally bisected into lobes. Locomotion ditaxic between lobes of foot. Eyes at base of tentacles; bifid snout produced into short secondary tentacles.

**Remarks:** This genus differs from *Clydonopoma* and *Chondropomella* in lacking a pseudolamellate operculum and in having deeply incised inner marginal radular teeth. Phylogenetic results corroborate the separation of *Chondropomium* from the other taxa reviewed here (Figure 5).

*Chondropomium* was originally described as a subgenus of *Chondropoma*, but was raised to generic status by Watters (2006). As defined here, *Chondropomium* is a Tiburon peninsular group. Most Tiburon annulariids are limited to that region but species of *Chondropomium* have colonized the rift valley and associated river valleys now separating that peninsula from the remainder of Hispaniola. It is perhaps significant that, with one exception, these colonizing taxa are limited to the xeric lowlands of these valleys, generally below 200 m, and have not yet adapted to the montane regions of remaining Hispaniola. The exception is *C. caelicum*, which occurs from 200–800 m in the mountains on either side of the Río San Juan valley.

Bartsch (1946) included *Chondropoma eusarcum* Pfeiffer, 1854, in *Chondropomium*. He recognized three subspecies; one from Puerto Plata, one from Isla Catalinita, and the nominate subspecies from an unlocalized region. A fourth, unnamed relative occurs in Altagracia Province. Puerto Plata and Isla Catalinita/Altagracia are separated by >270 km and it is highly unlikely that Bartsch's taxa are conspecific. All of these taxa resemble *Chondropomium* but are far removed from the Tiburon area and adjacent valleys. These species differ from *Chondropomium* in having lamellate axial sculpture, at least on early whorls, rather than flattened threads or cords. No material was available for phylogenetic study. Pending additional study these are here regarded as species of *Chondropoma* superficially similar to *Chondropomium*. Should they be found to belong to *Chondropomium* it would indicate that that group is much more widespread on the island than described here.

With few exceptions, members of *Chondropomium* live in very xeric habitats characterized by sparse vegetation (cacti, agave, thorny bushes, small clumps of grass) and rocky soils. They estivate under seemingly solidly embedded rocks or under dense mats of dead grasses and agave. They probably emerge during periods of rain or possibly at night. The nearly smooth shells have only weak axial sculpture that would minimize drag while burrowing and which seems to be an adaptation for this lifestyle.

Individuals are rarely found alone; a half dozen or more specimens of a species may be found under the same rock

and they may be locally abundant at a site. Estivating live individuals are often accompanied by numerous dead shells, suggesting that the snails either died of natural causes while estivating or were killed by some burrowing predator. Dead specimens often have drilled holes through the shell that may be the result of predation by the burrowing larvae of lampyrid and elaterid beetles.

Individuals of *Chondropomium* species show an unusually broad range of shell colors for the family. Within a population specimens may range from a nearly uniform dark color (often brown or orangish) with conspicuous markings to all white with no markings. This is particularly evident in *C. weinlandi*, discussed at length below.

Based on its position in the phylogenetic tree presented here (Figure 5), *Chondropomium* is one of the most recently derived members of the genera reviewed here. Like *Superbipoma*, the operculum has lost the ancestral pseudolamella and been reduced to a fine granular deposit.

### *Chondropomium beatense* (Clench, 1932)

(Figures 6–11, 183)

#### CHRESOONYMY

*Chondropoma* (*Chondropomium*) *beatensis* Clench, 1932: 106; Bartsch, 1946: 33–34, pl. 5, fig. 3.

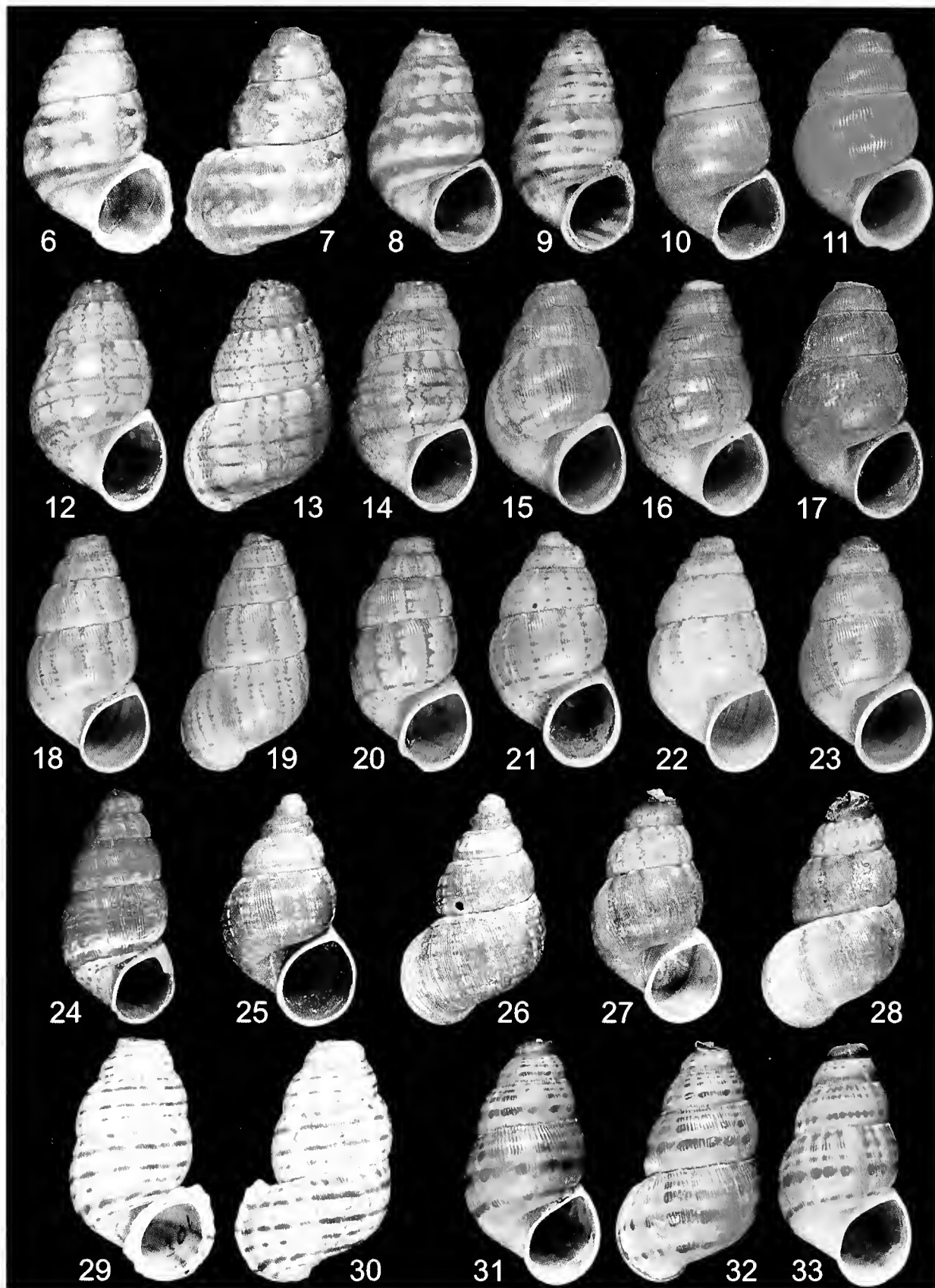
*Chondropoma* (*Chondropomella*) *beatensis* Clench, 1932: Bartsch, 1932: 3, pl. 1, figs. 7, 9.

*Chondropoma* (*Chondropomium*) *beatensis armouri* Clench, 1932: 106; Bartsch, 1932: 3 [in synonymy of *Chondropoma beatensis* Clench, 1932]; Bartsch, 1946: 33 [in synonymy of *Chondropoma beatensis* Clench, 1932]; Watters, 2006: 167 [in synonymy of *Chondropoma beatensis* Clench, 1932].

*Chondropoma* sp. indet.: Brooks, 1936: 124, text fig.

*Chondropomium beatense* (Clench, 1932): Watters, 2006: 63, 166.

**Description:** Shell medium for family (largest adult specimen 16.4 mm maximum length, decollate, including peristome; smallest adult specimen 9.5 mm length, decollate, including peristome), solid, conic, umbilicus small, narrow. Protoconch of 1.5 smooth whorls, not well-differentiated from teleoconch, rarely retained in adults. Teleoconch of 3.5–4 whorls, final whorl detached for last 1/6th of whorl. Suture narrow, channeled. Peristome single or rarely double, tear drop-shaped. Outer lip narrow, weakly expanded, minute posterior auricle present, narrowly detached from previous whorl. Spiral sculpture absent except for few very weak, almost obsolete cords within umbilicus. Axial sculpture of narrow, low ribs, separated by incised grooves, ca. 120 ribs on final whorl, forming minute serrations at suture. Background color very variable, from white to clouded with orange or yellow, often overlain with continuous or interrupted spiral brown bands, chevrons, and blotches; orange individuals may have faint pale, vertical zones; umbilicus and lip white. Operculum paucispiral with thin calcareous deposit. Anatomy and radula unknown.



**Figures 6–33.** *Chondropomium* species. **6–11.** *Chondropomium beatense* (Clench, 1932). **6, 7.** USNM 414227, paratype, 13.4 mm. **8.** UF 216536, 16.7 mm. **9.** UF 216536, 17.4 mm. **10.** *Chondropoma beatensis armouri* Clench, 1932. USNM 414228, paratype, 14.5 mm. **11.** UF 216539, 9.7 mm. **12–17.** *Chondropomium blaincorum* Watters, 2012. **12, 13.** UF 446070, holotype, 13.0 mm. **14.** UF 45726, 17.1 mm. **15.** UF 45726, 14.4 mm. **16.** UF 45726, 17.9 mm. **17.** UF 216507, 17.2 mm. **18–24.** *Chondropomium caelicum* new species **18, 19.** UF 216868, holotype, 18.9 mm. **20.** UF 505818, paratype 1, 17.1 mm. **21.** UF 505818, paratype 2, 14.4 mm. **22.** UF 505818, paratype 3, 17.1 mm. **23.** UF 505818, paratype 5, 14.9 mm. **24.** UF 216812, 16.3 mm. **25–28.** *Chondropomium gimbiense* (Bartsch, 1946). **25, 26.** *Chondropoma (Chondropomium) gimbiense gimbiense* Bartsch, 1946. USNM 471935, holotype, 10.2 mm. **27, 28.** *Chondropoma (Chondropomium) gimbiense saltroense* Bartsch, 1946. USNM 471936, holotype, 14.0 mm. **29, 30.** *Chondropomium ignotum* (Bartsch, 1946). USNM 471940, holotype, 16.6 mm. **31–33.** *Chondropomium lypix* Watters, 2012. **31, 32.** UF 446072, holotype, 19.6 mm. **33.** OSUM 36519, paratype, 19.0 mm.

**Type Material:** *Chondropoma beatensis* Clench, 1932: Holotype: MCZ 81493; Paratypes: MCZ 81494(?); USNM 414227(2) (but not listed as types in database); ANSP 157702(2). Clench (1932) only listed four paratypes, without catalog numbers or collection identification; it is not clear which of the MCZ, USNM, or ANSP specimens are actual paratypes; *Chondropoma beatensis armouri* Clench, 1932: Holotype: MCZ 81495; Paratype: USNM 414228(1).

**Type Locality:** *Chondropoma beatensis* Clench, 1932: "Beata Island, Santo Domingo." *Chondropoma beatensis armouri* Clench, 1932: "Beata Island."

**Type Figured:** *Chondropoma beatensis* Clench, 1932: unfigured. *Chondropoma beatensis armouri* Clench, 1932: unfigured.

**Distribution:** Endemic to Isla Beata, a uninhabited island off the Barahona Peninsula.

**Habitat:** Coastal limestone cliffs.

**Other Material Examined (152 Specimens): Dominican Republic.** GTW 7261a(1), NE part of Isla Beata; USNM 414227(2), USNM 414228(1), UF 216536 (23), UF 216537(71), UF 216538(8), Isla Beata; UF 216539(46), N point, Isla Beata.

**Variation Among Specimens:** Specimens appear to come in two color forms with intergradation. One form has brown patterns on a white background, the other is lacks a pattern or nearly so, with a yellow or orange background.

**Comparison with Other Species:** This species is most similar to *C. blaineorum* Watters, 2012, but differs in the more diffuse, less defined color pattern that is not arranged in a mosaic configuration.

**Remarks:** *Chondropoma beatensis armouri* was described for the orange, patternless color form; we do not consider it distinct. Other Hispaniolan annulariid species, originally believed to be endemic to an island, have subsequently been found on the adjacent mainland: *Abbottella milleacantha* Watters and Duffy, 2010, described from Isla Saona, and *Colonina dominicensis* (Pfeiffer, 1850) from Isla Catalina have both been found on the coastal mainland (Watters and Frank-Fellner, 2017). However, *C. beatense* has not been found on the adjacent mainland as yet. No material was available for phylogenetic study.

**Etymology:** As the root endings *-poma* and *-pomium* are neuter, the correct orthography should be *beatense*. *Chondropoma beatense* Clench, 1932: Isla Beata, Dominican Republic. *Chondropoma beatense armouri* Clench, 1932: Allison V. Armour (1863–1941), archeologist, botanist, herpetologist associated with the Chicago Field Museum; his yacht *Utowana*, a one time fishing trawler and WW I Atlantic escort craft, visited Isla Beata on 14–15 February 1929 where Thomas Barbour of MCZ

collected the types of both of these taxa. An excellent account of the expedition is found in Henderson and Powell, 2004.

### ***Chondropomium blaineorum* Watters, 2012** (Figures 12–17, 182)

CHRESOXYMY:

*Chondropomium blaineorum* Watters, 2012: 9, figs. 34, 35.

**Description:** Shell medium to small for family (largest adult specimen 18.0 mm maximum length, decollate, including peristome; smallest adult specimen 12.9 mm length, decollate, including peristome), solid, conic, umbilicus minute. Protoconch whorls unknown, decollate in all specimens examined. Teleoconch of 3–3.5 whorls, final whorl detached for last 1/6th of whorl. Suture narrowly channeled. Peristome single or weakly double, tear drop-shaped. Outer lip narrow, not expanded, minute posterior auricle present. Spiral sculpture present only as 7–8 very feeble cords within umbilicus. Axial sculpture of narrow, closely-spaced, low ribs, nearly obsolete on final whorl, forming minute cusps at suture. Suture serrate. Background color pale tan to brown with narrow darker bands having zigzag markings between them axially arranged into tile-like pattern; umbilicus and lip white. Operculum paucispiral with thin calcareous deposit. Anatomy and radula unknown.

**Type Material:** Holotype: UF 446070; Paratype: OSUM 36516(1).

**Type Locality:** "ca. 9.3 km NW of Manuel Golla, ca. 140 m, off Highway 44, Pedernales Province, Dominican Republic. 17.94 N, -71.65 W."

**Type Figured:** Watters, 2012, figs. 34, 35.

**Distribution:** With a single exception at Laguna de Oviedo, all specimens have been collected along RD Highway 44 between Pedernales and Oviedo. This road runs along the southern foothills of the Sierra Baoruco, from nearly sea level to 200 m.

**Habitat:** Under rocks on hillsides with limestone outcrops.

**Other Material Examined (86 Specimens): Dominican Republic. Pedernales Province.** UF 216457a(2), 8 km SE of Pedernales; UF 216400(2), 23 km SE of Pedernales; UF 216505(21), 26 km NW of Oviedo; UF 45726(7), UF 216507(9), 18 km NW of Oviedo; UF 216779(3), UF 216780(3), 17 km NW of Oviedo; UF 216778(26), 13 km NW of Oviedo; GTW 7082c(2), 10 km NW of Oviedo; UF 216781(1), 8 km NW of Oviedo; UF 216773a(12), 7.5 km NW of Oviedo; UF 467467(2), S end of Laguna de Oviedo.

**Variation Among Specimens:** The peculiar mosaic or tile-like color pattern varies from well-developed to

smudged and indistinct depending on the background color.

**Comparison With Other Species:** This species is very similar to *Chondropoma quisquense* Bartsch, 1946, in color patterns and shape and may be sympatric with it in some places, but lacks the spiral sculpture of that species. It is also sympatric with *Chondropomum marmoreum* but lacks the spiral threads on the spire. See also under *C. beatense*.

**Remarks:** The original images of this species in 2012 were unfortunately vertically foreshortened by the printer. No material was available for phylogenetic study.

**Etymology:** Matt and Dona Blaine (Delaware, USA), who helped collect the type lot.

***Chondropomum caelicum* new species**  
(Figures 18–24, 184)

**Description:** Shell medium to small for family (largest adult specimen 19.8 mm maximum length, decollate, including peristome; smallest adult specimen 12.0 mm length, decollate, including peristome), solid, conic, polished, umbilicus small, narrow. Protoconch unknown, decollated in all examples seen, not retained in adults. Teleoconch of 3.75–4.25 whorls, final whorl detached for last 1/8th of whorl. Suture narrow, channeled. Peristome single, tear drop-shaped. Lip narrow, very weakly expanded, posterior auricle absent, narrowly detached from previous whorl, forming short keel posteriorly. Spiral sculpture absent except for few very weak, almost obsolete cords within umbilicus. Axial sculpture of flat, low ribs, separated by incised grooves, ca. 120 ribs on final whorl, forming minute serrations at suture; no fused tufts. Axial ribs gathered into growth series having ca. 10 ribs/series. Background color very variable, base color from white to clouded with orange or yellow; brown axial bands on trailing edge of growth series have regular triangular or dashed markings that form interrupted spiral pattern; shell usually pale overall but rarely darkly colored. Umbilicus and lip white. Operculum paucispiral with thin calcareous deposit. Anatomy and radula unknown.

**Type Material:** Holotype: UF 216868, 18.9 mm; Paratype 1: UF 505818, 17.1 mm; Paratype 2: UF 505818, 14.4 mm; Paratype 3: UF 505818, 17.1 mm; Paratype 4: UF 505818, 13.4 mm; Paratype 5: UF 505818, 14.9 mm.

**Type Locality:** 200 m elevation, 2 km NW of Cortés, San Juan Province, Dominican Republic.

**Distribution:** From 200–800 m, in calcareous regions of the Cordillera Central and the Sierra de Neiba bordering the Río San Juan and Río Macasía valleys.

**Habitat:** Found under limestone blocks in sub-mesic scrub and in mesic forest.

**Other Material Examined (134 Specimens): Dominican Republic. San Juan Province.** UF 216868(42),

200 m, 2 km NW of Cortés; UF 216807(42), 450 m, 1 km SSW of Cardón; UF 216841(1), 780 m, 5 km S of Vallejuelo; UF 216819(7), 710 m, 4 km E of Vallejuelo; UF 216812(21), 540 m, 4 km SW of Cardón on road to Vallejuelo; UF 216818(1), 690 m, 15 km NNW of Juan de Herrera; UF 216820(1), 540 m, 4 km NW of Bohechio. **La Estrelleta Province.** UF 216806(18), 790 m, 6 km SW of Hondo Valle.

**Variation Among Specimens:** As in *Chondropomum weinlandi*, this species shows great variation in color pattern but unlike that species the patterns form a continuum and do not seem to be separated into “forms.”

**Comparison With Other Species:** *Chondropomum caelicum* new species is most similar to *C. weinlandi*. It differs in having the color pattern axially arranged rather than spirally aligned; *C. weinlandi* rarely has axial color elements.

**Remarks:** This species is unique in several regards. It has colonized the furthest from the Tiburon Peninsula of all of the taxa reviewed here. It continues from the range of *C. weinlandi* north into the valleys of the Río San Juan and Río Macasía. But unlike *C. weinlandi* and other *Chondropomum* it occurs in upland sub-mesic and mesic forests rather than xeric lowlands. No material was available for phylogenetic study.

**Etymology:** *L. caelicum*, heavenly, for its comparatively montane habitat.

***Chondropomum gimbiense* (Bartsch, 1946)**  
(Figures 25–28, 184)

CHRESOXYMY

*Chondropoma* (*Chondropomum*) *gimbiense gimbiense* Bartsch, 1946: 34, 35, pl. 6, fig. 3.

*Chondropoma* (*Chondropomum*) *gimbiense saltronense* Bartsch, 1946: 34, pl. 6, fig. 2.

*Chondropomum gimbiense* (Bartsch, 1946): Watters, 2006: 63.

*Chondropomum gimbiense gimbiense* (Bartsch, 1946): Watters, 2006: 272.

*Chondropomum gimbiense saltronense* (Bartsch, 1946): Watters, 2006: 272.

*Licina gimbiensis* (Bartsch, 1946): Watters, 2013: map 1.

**Description:** Shell small for family (largest adult specimen 14.0 mm maximum length, decollate, including peristome; smallest adult specimen 10.2 mm length, non-decollate, including peristome), solid, conic, umbilicus minute. Protoconch whorls of 1.5 smooth, minute whorls, usually decollate in adults. Teleoconch of 4 whorls, final whorl only shortly detached before aperture, forming short posterior keel. Suture minutely channeled. Peristome weakly double, tear drop-shaped. Peristome double. Inner lip not erect, fused to outer lip; outer lip narrow, not expanded, minute posterior auricle present. Spiral sculpture present only as few very feeble cords within umbilicus. Axial sculpture of numerous, narrow,

closely-spaced, low ribs, separated by narrow incised grooves, forming minute cusps at suture; slightly enlarged cusps occur in groups of 5–6 at irregular intervals. Background color white to brownish-purple with tan axial zig-zags; these markings may be spirally aligned on earlier whorls; early whorls may be darkly colored; umbilicus and lip white; interior of aperture brown in some specimens. Operculum paucispiral with thin calcareous deposit. Anatomy and radula unknown.

**Type Material:** *Chondropoma* (*Chondropomium*) *gimbiense gimbiense* Bartsch, 1946: Holotype: USNM 471935. *Chondropoma* (*Chondropomium*) *gimbiense saltrouense* Bartsch, 1946: Holotype: USNM 471936.

**Type Locality:** *Chondropoma* (*Chondropomium*) *gimbiense gimbiense* Bartsch, 1946: “East bank of the Rivière Gimbi in the vicinity of Saltrou.” *Chondropoma* (*Chondropomium*) *gimbiense saltrouense* Bartsch, 1946: “West side of the Rivière Gimbi.”

**Type Figured:** *Chondropoma* (*Chondropomium*) *gimbiense gimbiense* Bartsch, 1946: Bartsch, 1946, pl. 6, fig. 3. *Chondropoma* (*Chondropomium*) *gimbiense saltrouense* Bartsch, 1946: Bartsch, 1946, pl. 6, fig. 2.

**Distribution:** Known only from the Rivière Gimbi valley in the vicinity of Saltrou (now Belle-Anse) in the Sud-Est Department of Haiti on the southern coast of the Tiburon Peninsula.

**Habitat:** Not reported.

**Other Material Examined (19 Specimens):** Haiti. **Département du Sud-Est.** USNM 471936(10), W side of the Rivière Gimbi; USNM 402015(9), E bank of the Rivière Gimbi in the vicinity of Saltrou.

**Variation Among Specimens:** Specimens differ in the depth of background coloration and degree of elongation.

**Comparison With Other Species:** This species differs from its congeners in its combination of silky texture and vertically aligned color pattern. In this respect it resembles some *Crosseopoma*, but is differentiated from that genus by its non-pseudolamellate operculum. It is geographically distant from any other known congener.

**Remarks:** No material was available for phylogenetic study.

**Etymology:** *Chondropoma* (*Chondropomium*) *gimbiense gimbiense* Bartsch, 1946. Rivière Gimbi, Haiti. *Chondropoma* (*Chondropomium*) *gimbiense saltrouense* Bartsch, 1946. Saltrou, Haiti.

***Chondropomium ignotum* (Bartsch, 1946)**  
(Figures 29, 30)

CHRESOXYMY

*Chondropoma* (*Chondropomium*) *ignotum* Bartsch, 1946: 31, pl. 5, fig. 7.

*Chondropomium ignotum* (Bartsch, 1946): Watters, 2006: 63, 300.

**Description:** Shell medium for family (only known specimen 16.6 mm maximum length, decollate, including peristome), solid, inflated conic, umbilicus minute. Protoconch unknown, decollate. Teleoconch of 3.25 whorls, final whorl only shortly detached before aperture, forming short posterior keel. Suture narrowly channeled. Peristome double, oval. Inner lip narrowly erect, not fused to outer lip; outer lip evenly expanded, fairly wide, low posterior auricle present. Spiral sculpture present only as well-developed cords within umbilicus. Axial sculpture of numerous (ca. 120), wide, closely-spaced, flattened ribs, separated by narrow incised grooves, forming irregular, minute cusps at suture. Background color white with seven tan, spiral bands alternating between spots and nearly continuous bands on final whorl; last band borders umbilicus; some bands continue onto both sides of lip. Operculum, anatomy, and radula unknown.

**Type Material:** Holotype: USNM 471940.

**Type Locality:** “Haiti?”

**Type Figured:** Bartsch, 1946, pl. 5, fig. 7.

**Distribution:** Described from “Haiti?” without further information.

**Habitat:** Not reported.

**Variation Among Specimens:** Known only from the holotype specimen.

**Comparison With Other Species:** This species is known from the single, unlocalized holotype specimen. It clearly is related to taxa such as *C. weinlandi* and *C. caelicum* but the expanded outer lip is unique. *Superbipoma* species also have an expanded lip, but the lip of *C. ignotum* is double with a narrow, distinct lamella rather than a reflected portion of a single lip as in *Superbipoma*.

**Remarks:** Although it possibly is a teratological individual of another species, we believe it is distinct but awaiting rediscovery. No material was available for phylogenetic study.

**Etymology:** *L. ignotus*, strange, unnoticed.

***Chondropomium lynx* Watters, 2012**  
(Figures 31–33, 182)

CHRESOXYMY

*Chondropomium lynx* Watters, 2012: 10–11, figs. 39–41, not 58 [habitat, mislabeled locality].

**Description:** Shell medium for family (largest adult specimen 19.6 mm maximum length, decollate, including peristome; smallest adult specimen 19.0 mm length,

decollate, including peristome), solid, conic, umbilicus minute. Protoconch whorls unknown, decollate in all specimens examined. Teleoconch of 4 whorls, final whorl detached for last 1/4th of whorl. Suture narrowly channeled. Peristome single, tear drop-shaped. Lip narrow, not expanded, minute posterior auricle present, detached from previous whorl. Spiral sculpture present only as ca. 3 very feeble cords within umbilicus. Axial sculpture of numerous (ca. 90) fairly wide, closely-spaced, low ribs, strongest on last 1/4 of final whorl, forming minute cusps at suture. Background color pale tan with 5 interrupted bands, 3 above, one at, and one below periphery, composed of dark brown spots, blurred and repeated; first teleoconch whorl dark brown; lip white. Operculum paucispiral with thin calcareous deposit. Anatomy and radula unknown.

**Type Material:** Holotype: UF 446072; Paratypes: OSUM 36518(1); OSUM 36519(1).

**Type Locality:** Originally described from the area of Virgen de San Rafael and Los Patos in Barahona Province, these specimens are now known to have been mislabeled. The type locality (and that of all known specimens) is here corrected to Dominican Republic, Peravia Province, Punta Salina, 21 km W of Bani. This site is just north of RD 2 (Carretera Francisco del Rosario Sánchez) on a series of low hills on the west bank of the Río Ocoa.

**Type Figured:** Watters, 2012, figs. 39, 40.

**Distribution:** Known only from the area of the type locality.

**Habitat:** Under rocks on low xeric hills (< 200 m) with cacti and agave. This species co-occurs with *Tessaripoma hooksi* (Watters and Duffy, 2010) but appears to be much rarer.

**Other Material Examined (6 Specimens):** GTW 16671a(2), GTW 16671b(2), GTW 16671c(2), all from the type locality.

**Variation Among Specimens:** The few known specimens are very uniform in characteristics, varying mainly in the degree of background coloration.

**Comparison With Other Species:** *Chondropomium lynx* is very similar to *C. weinlandi*, particularly the color form known as *barahonensis*. It differs in its more elongate shape, dark early whorls, and different banding pattern. It occurs at the extreme eastern end of the range of *C. weinlandi*.

**Remarks:** The original images of this species in 2012 were unfortunately vertically foreshortened by the printer. No material was available for phylogenetic study.

**Etymology:** *Lynx rufus*, the American bobcat or lynx; the shell has a similar color pattern. Used as a noun in apposition.

***Chondropomium marmoreum* (Watters and Duffy, 2010)**  
(Figures 3, 4, 34–42, 184)

#### CHRESONYMY

*Chondropoma* (*Chondropoma*) *marmoreum* Watters and Duffy, 2010: 6–7, figs. 16–19.

*Chondropoma marmoreum* Watters and Duffy, 2010: Watters, 2012: 9, 14, figs. 51, 52, 55 [habitat], 56 [habitat].

**Description:** Shell medium for family (largest adult specimen 18.3 mm maximum length, decollate, including peristome; smallest adult specimen 14.0 mm length, decollate, including peristome), solid, conic, umbilicus minute. Protoconch whorls unknown, decollate in all specimens examined. Teleoconch of 4.25 whorls, final whorl detached immediately before lip. Peristome double, tear drop-shaped. Outer lip thin, narrow to moderately expanded, minute posterior auricle present, lip detached from previous whorl. Inner lip short, mostly fused with outer lip. Spiral sculpture of numerous (ca. 36 on final whorl) low threads or cords, becoming stronger and more widely separated towards umbilicus; 3–6 very feeble cords within umbilicus. Axial sculpture of similar sized threads. Intersections of sculpture forming minutely beaded surface. Suture minutely channeled. Axial threads forming minute cusps at suture. Background color tan, reddish brown, or grey, with dark brown “D”-shaped spots arranged in spiral bands, often aligned into axial stripes as well; lip white. Operculum paucispiral with thin calcareous deposit. Radula as in genus but with strong hook-shaped denticle on inner side. Animal unknown.

**Type Material:** Holotype: UF 420735; Paratypes: OSUM 32483(1); OSUM 32482(1); BMNH 1996347(1).

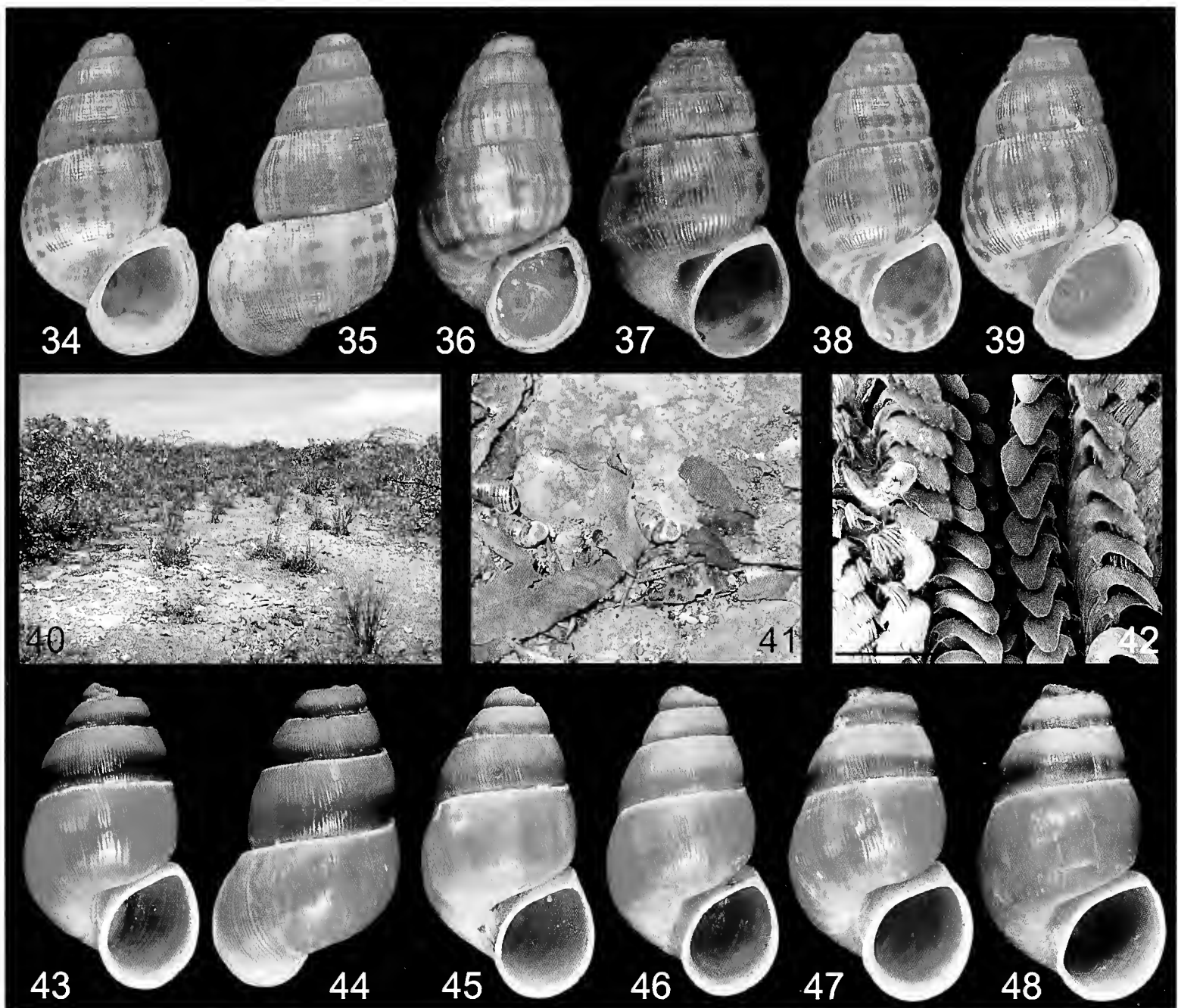
**Type Locality:** “Dominican Republic, Barahona Peninsula, Pedernales Province, along Route 44 ca. 10 km SE of Pedernales.”

**Type Figured:** Watters and Duffy, 2006, figs. 16, 17.

**Distribution:** Low hills off the western Sierra Baoruco from Pedernales down the coast to Cabo Rojo and southeast almost to Oviedo.

**Habitat:** Under limestone debris in xeric areas with cacti, often near the coast. Locally abundant.

**Other Material Examined (688 Specimens): Dominican Republic. Pedernales Province.** UF 216776 (10), 5 km NW of Oviedo; UF 216774(26), 8 km NW of Oviedo; UF 216419(9), 8 km SW of Las Mercedes; UF 216391(9), 6 km SW of Las Mercedes; UF 216460(66), 15 km SE of Pedernales; UF 216465(52), 20 m, 17 km SE of Las Mercedes; UF 216459(74), 26 km NW of Oviedo; GTW 7170a(1), 22.5 km W of Oviedo; GTW 7170b(1), Cabo Falso; UF 216510(32), Cabo Rojo; UF 216458(43), 13 km N of Cabo Rojo; GTW 7170c(15), 3.4 m, just N of Cabo Rojo airport; UF 216499(12), 6 km SSE of Cabo Rojo; GTW 7170d(3), along RD 44, next to large limestone outcrops, 16 km E of Cabo Rojo; UF 216388(150), UF 249174(19), 3 km SE of Cabo Rojo; UF 216457(69), UF 216514(25), 8 km SE of Pedernales; GTW 7170e(3), 10 km SE of Pedernales off RD 44; UF



**Figures 34–48.** *Chondropomium* species. 34–42. *Chondropomium marmoratum* (Watters and Duffy, 2010). 34, 35. UF 420735, holotype, 18.3 mm. 36. UF 216459, 17.7 mm. 37. UF 216776, 15.4 mm. 38. BMNH 1996347, paratype, 18.3 mm. 39. OSUM 32483, paratype, 15.4 mm. 40. Habitat (photo A. Gettleman). 41. Individuals *in situ* under rock (photo A. Gettleman). 42. GTW 77170d, radula. Scale bar = 100  $\mu$ m. 43–48. *Chondropomium sardonix* new species. 43, 44. UF 216454, holotype, 19.3 mm. 45. UF 505805, paratype 1, 19.1 mm. 46. UF 505805, paratype 2, 17.3 mm. 47. UF 505805, paratype 5, 15.8 mm. 48. UF 467518, 20.1 mm.

216465(17), UF 216512(20), UF 257730(44), 17 km SE of Pedernales; UF 216501(29), 22 km SE of Pedernales; GTW 7170f(3), 15–16 km E of Cabo Rojo off RD 44; GTW 7170g(1), 0.7–1.1 km along 5 km rough road that runs from 1.9 km S of old naval base to La Cueva, Cabo Rojo.

**Variation Among Specimens:** The dark brown color pattern varies from a few axially aligned triangles to more extensive mottling.

**Comparison With Other Species:** This species has a color pattern similar to some specimens of *C. blaincorum* (with which it may be sympatric) and *C. weinlandi*. It

differs from all other species in the genus by possessing distinct spiral sculpture on at least the early whorls, which may render the surface beaded or even minutely serrate. It is also similar to *Chondropoma eyerdami* Bartsch, 1946, from the Tiburon Peninsula of Haiti, and *Chondropoma brownianum* Weinland, 1880, from Île de la Gonâve, Haiti. It differs from both in having weaker sculpture.

**Remarks:** This species is placed in *Chondropomium* with some reservation. The finely beaded sculpture is more similar to *Chondropoma*, but the shell form and coloration are more like *Chondropomium*. The radula differs from other *Chondropomium* studied in having a prominent

hook-shaped denticle on the inner side of the inner marginal tooth; this is lacking in other species covered here. Along with *C. eyerdami* and *C. brownianum*, it may prove to be a member of an undescribed genus apart from either *Chondropoma* or *Chondropomium*. Unfortunately, no suitable genetic material was available for study for any of these taxa.

**Etymology:** *L. marmoreus*, marbled.

***Chondropomium sardonix* new species**

(Figures 43–48, 182)

**Description:** Shell medium for family (largest adult specimen 20.1 mm maximum length, decollate, including peristome; smallest adult specimen 15.0 mm length, decollate, including peristome), translucent but solid, stout, elongate conic, polished. Protoconch unknown; all specimens seen decollate. Teleoconch of 3.75–4 whorls. Axial sculpture of final whorl of numerous (ca. 120) very fine, closely spaced, low, weak threads, often obscure. Spiral sculpture absent except for ca. 15 cords within umbilicus. Overall sculpture very weak, with polished aspect. Suture narrowly channeled. Each axial thread slightly enlarged into bead at suture, rendering suture minutely serrate. Aperture teardrop-shaped, lip single, not or very slightly expanded, posteriorly angulate but lacking auricle. Lip narrowly detached from previous whorl for ca. ¼ turn, angular posterior of lip forming sharp crest. Color pattern of final whorl reddish-orange with white umbilicus; previous whorls tan posteriorly and dark purple anteriorly. Lip white inside and out. Sutural beads white, contrasting with purple of previous whorl and orange of final whorl. Operculum paucispiral with thin calcareous deposit. Animal and radula unknown.

**Type Material:** Holotype: UF 216454; Paratype 1: UF 505805; Paratype 2: UF 505805; Paratype 3: UF 505805; Paratype 4: UF 505805; Paratype 5: UF 505805.

**Type Locality:** 20 m elevation, 3 km ESE of La Canoa, Barahona Province, Dominican Republic.

**Distribution:** Known only from the western foothills of the Sierra Martín García, an isolated outlier of the Sierra Neiba.

**Habitat:** Specimens were found in a xeric arroyo under agave. Locally common.

**Other Material Examined (43 Specimens): Dominican Republic. Barahona Province.** UF 505806(36), from the type locality; UF 467518(5), 1.6 km W of Fondo Negro; UF 216822(2), 200 m, 12 km NE of La Canoa.

**Variation Among Specimens:** Specimens are very uniform in most characteristics, but differ in the degree of coloration.

**Comparison With Other Species:** The overall coloration of this rarely seen species is unique in the genus.

However, the color pattern is very similar to that found in some *Colonina*, but *C. sardonix* lacks the prominent sutural tufts of those species.

**Remarks:** This species is sympatric in its very narrow range with the color forms *azuense* and *barahonense* of *C. weinlandi*. It is known only from dead specimens.

**Etymology:** Named for the form of the mineral onyx having red parallel bands: *sardonix*; a noun in apposition.

***Chondropomium weinlandi* (Pfeiffer, 1862)**

(Figures 49–73, 185)

CHRESOONYMY

**“*weinlandi* form”**

*Cyclostoma semilabre* “Lamarck” of Pfeiffer, 1850: 80 [misidentification]; Pfeiffer, 1854b: 271, pl. 37, figs. 1, 2; Pfeiffer, 1854d: pl. 49, fig. 17; Crosse, 1891: 172; Bartsch, 1946: 27 [in synonymy of *Chondropoma weinlandi* Pfeiffer, 1862] [non Lamarck, 1822].

*Chondropoma semilabre* “Lamarck” of Pfeiffer, 1851: 173 [misidentification]; Pfeiffer, 1852a: 286; Adams and Adams, 1858: 295, pl. 86, figs. 11a, b; Pfeiffer, 1858b: 139; Reeve, 1863: text to pl. 1, figs. 2a, b [in synonymy of *Chondropoma weinlandi* Pfeiffer, 1862]; Bartsch, 1946: 27 [in synonymy of *Chondropoma weinlandi* Pfeiffer, 1862] [non Lamarck, 1822].

*Chondropoma weinlandi* Pfeiffer, 1862: 96–97; Reeve, 1863: text to pl. 1, fig. 2a; Pfeiffer, 1865: 149; Pfeiffer, 1876: 193; Kobelt, 1880: 277; Weinland, 1880: 342–343, 346, 347; Crosse, 1891: 167, 172–173; Clench and Aguayo, 1948: 54.

*Chondropoma* (*Chondropomium*) *weinlandi* Pfeiffer, 1862: Henderson and Bartsch, 1920: 59–60; Pilsbry, 1933: 126, 129; Wenz, 1939: 542, fig. 1441.

*Chondropoma* [*Chondropomium*] *weinlandi* Pfeiffer, 1862: Thiele, 1929: 131.

*Chondropoma* (*Chondropomium*) *swiftii swiftii* “Shuttleworth” Bartsch, 1946: 24–26, 28, pl. 4, figs. 1, 2.

*Chondropoma* (*Chondropomium*) *swiftii weinlandi* Pfeiffer, 1862: Bartsch, 1946: 27–28, pl. 4, fig. 5.

*Chondropoma semilabris* “Lamarck” of Pfeiffer, 1850: Mermod, 1952: 42–44, fig. 109.

*Chondropomium swiftii* “Shuttleworth” of Bartsch, 1946: Watters, 2006: 63, 498–499; Watters and Duffy, 2010: 7; Watters, 2012: 11.

*Chondropomium swiftii weinlandi* (Pfeiffer, 1862): Watters, 2006: 63, 547–548; Watters, 2012: 9, fig. 42.

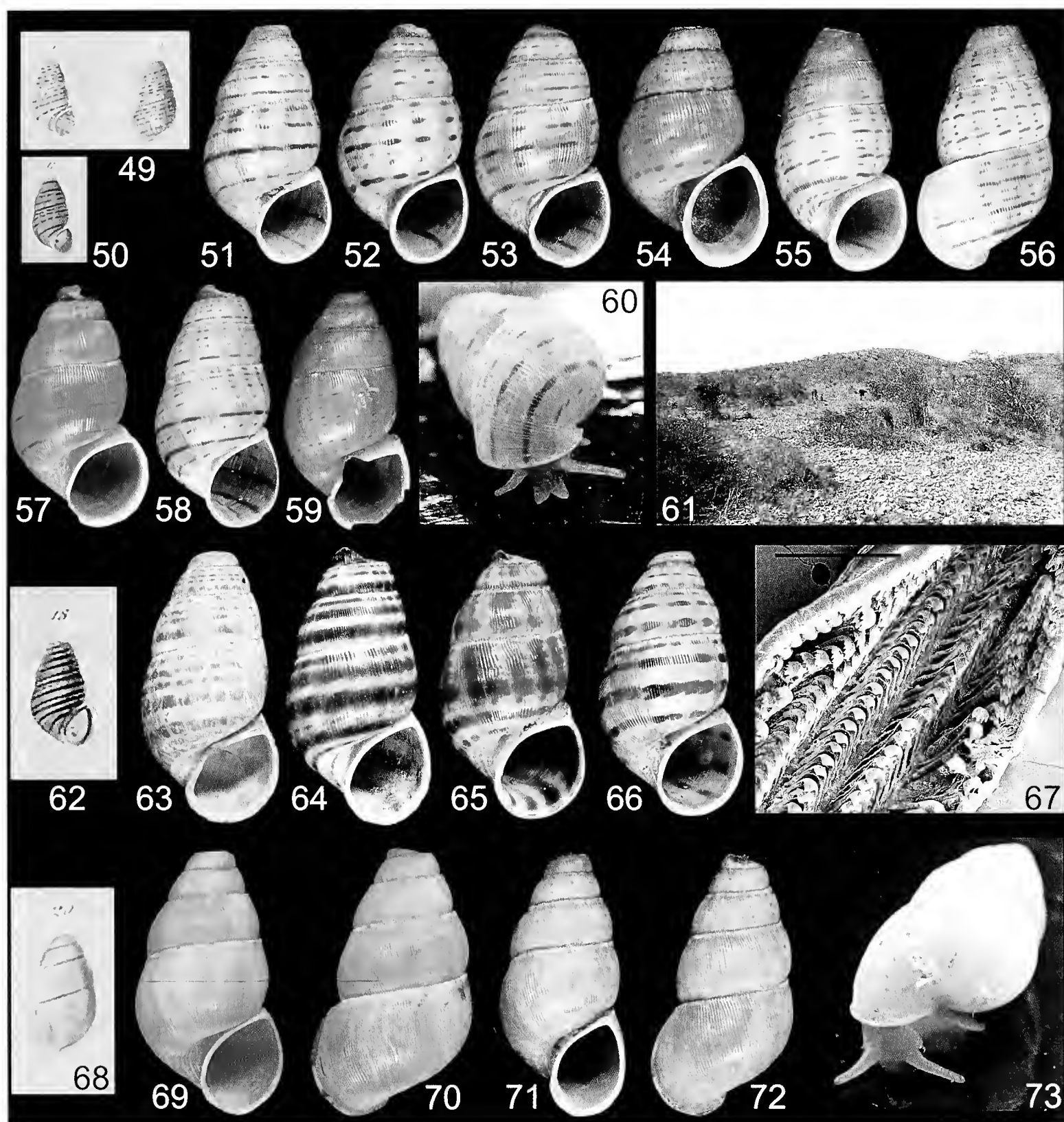
**“*azuense* form”**

*Cyclostoma semilabre* “Lamarck” of Pfeiffer, 1854d: pl. 49, fig. 20 [misidentification, non Lamarck, 1822].

*Chondropoma weinlandi* Pfeiffer, 1862: 96–97; Reeve, 1863: text to pl. 1, fig. 2b.

*Chondropoma* (*Chondropomium*) *swiftii azuense* Bartsch, 1946: 26, 29, pl. 4, fig. 6.

*Chondropomium swiftii azuense* (Bartsch, 1946): Watters, 2006: 63, 499.



**Figures 49–73.** *Chondropomum weinlandi* (Pfeiffer, 1862). 49–61. “*weinlandi* form”. 49. *Cyclostoma semilabre* “Lamarck” Pfeiffer, 1854b, pl. 37, figs. 1, 2. 50. *Cyclostoma semilabre* “Lamarck” Pfeiffer, 1854d: pl. 49, fig. 17. 51. UF 45658, 20.4 mm. 52. UF 45651, 19.0 mm. 53. UF 45654, 19.0 mm. 54. UF 216811, 15.5 mm. 55, 56. OSUM 42378, 12.0 mm. 57. OSUM 42361, 18.8 mm. 58. GTW 7087c, 17.5 mm. 59. GTW 7087c, 20.7 mm. 60. Living individual. 61. Habitat. 62–67. “*barahonense* form”. 62. *Cyclostoma semilabre* “Lamarck” Pfeiffer, 1854d: pl. 49, figs. 18. 63. *Chondropoma* (*Chondropomium*) *swiftii barahonense* Bartsch, 1946. USNM 354956, holotype, 18.9 mm. 64. *Chondropoma* (*Chondropomium*) *swiftii saturatum* Bartsch, 1946. USNM 354953, holotype, 16.6 mm. 65. UF 45651, 16.5 mm. 66. UF 45651, 19.2 mm. 67. OSUM 42362, radula. Scale bar = 200  $\mu$ m. 68–73. “*azucense* form”. 68. *Cyclostoma semilabre* “Lamarck” Pfeiffer, pl. 49, fig. 20. 69, 70. *Chondropoma* (*Chondropomium*) *swiftii azucense* Bartsch, 1946. USNM 493295, holotype, 19.0 mm. 71, 72. UF 216834, 18.3 mm. 73. Living individual.

**“barahonense/saturatum form”**

*Cyclostoma semilabre* “Lamarek” of Pfeiffer, 1854d: Pfeiffer, 1854d: pl. 49, fig. 18 [misidentification, *non* Lamarek, 1822].

*Chondropoma (Chondropomium) swiftii barahonense* Bartsch, 1946: 26–27, pl. 4, fig. 3.

*Chondropomium swiftii barahonense* (Bartsch, 1946): Watters, 2006: 63, 499; Watters, 2012: 11.

*Chondropoma (Chondropomium) swiftii saturatum* Bartsch, 1946: 26, pl. 4, fig. 4.

*Chondropomium swiftii saturatum* (Bartsch, 1946): Watters, 2006: 63, 499; Watters, 2012: 11.

**Description:** Shell medium for family (largest adult specimen 25.5 mm maximum length, decollate, including peristome; smallest adult specimen 14.1 mm length, decollate, including peristome), solid, polished, almost translucent, conic to fairly high-spined, umbilicus narrow, compressed, spire  $\frac{1}{2}$ – $\frac{1}{3}$  total length. Protoconch of 1.5 minute, smooth, pale tan whorls, decollated in adults. Decollate specimens have jagged, irregular break from earlier whorls, which seems to involve more than just protoconch whorls. Teleoconch of 3.75–4.5 whorls, final whorl narrowly detached for last  $\frac{1}{4}$ th of whorl. Suture narrow, channeled. Peristome single, tear drop-shaped. Lip barely expanded, narrowest facing umbilicus, with minute triangular posterior auricle, narrowly detached from previous whorl, forming sharp posterior keel. Spiral sculpture absent except for 8–17 narrow, fine cords within umbilicus. Axial sculpture of flattened, low ribs, separated by incised grooves, often grouped in growth series, ca. 130 ribs on final whorl, each forming minute bead at suture; no fused tufts present. Color pattern very variable; see Remarks below. Operculum paucispiral with thin calcareous deposit. Radula as in genus.

**Type Material:** *Chondropoma weinlandi* Pfeiffer, 1862: three specimens from NHMUK, unnumbered, from Cuming collection from “Haiti I.,” none bear an “X,” but may be the syntype lot. However, J. Ablett (pers. comm., 2016, NHMUK) does not believe that any of these are Pfeiffer’s material as they lack Pfeiffer’s handwriting and the label does not specify that they were collected by Sallé. Pfeiffer originally identified his specimens as *Cyclostoma semilabre* “Lamarek” (see Remarks below) but these specimens have not been found at NHMUK. Three other specimens glued on a board at NHMUK, also unnumbered, from Cuming collection labeled “*weinlandi* VAR” may be syntypes of Weinland’s variety *major* or variety *malleata* but this cannot be determined. A specimen at ZMB of *C. weinlandi* (65684) is from Pfeiffer but is labeled “kleiner als typus” (smaller than the type) on a second label; a second specimen labeled *C. weinlandi* (ZMB unnumbered) is from Paetel rather than Sallé; neither can be identified as type material (*C. Zorn*, pers. comm., 2016, ZMB), although apparently a type existed at some point. *Chondropoma (Chondropomium) swiftii azuense* Bartsch, 1946: Holotype: USNM 493298. *Chondropoma (Chondropomium) swiftii barahonense* Bartsch, 1946: Holotype: USNM 354956. *Chondropoma*

(*Chondropomium*) *swiftii saturatum* Bartsch, 1946: Holotype: USNM 493299; Paratype: USNM 354953.

**Type Locality:** *Chondropoma weinlandi* Pfeiffer, 1862: “Haiti.” *Chondropoma (Chondropomium) swiftii azuense* Bartsch, 1946: unknown, but collected by Sallé, who only collected in the Dominican Republic portion of Hispaniola. Bartsch (1946) listed Azua, Dominican Republic, for a non-type specimen. *Chondropoma (Chondropomium) swiftii barahonense* Bartsch, 1946: “Barahona.” *Chondropoma (Chondropomium) swiftii saturatum* Bartsch, 1946: unknown.

**Type Figured:** *Chondropoma weinlandi* Pfeiffer, 1862: Pfeiffer (1862), in a list of misidentifications of *C. semilabris* that he subsequently reidentified as *C. weinlandi*, gave Pfeiffer, 1854b, pl. 37, figs. 1, 2 and 1854d, pl. 49, figs. 17–20, as the only figured specimens, but see Remarks. No one figure can be identified with Pfeiffer’s description. *Chondropoma (Chondropomium) swiftii azuense* Bartsch, 1946: Bartsch, 1946, pl. 4, fig. 6. *Chondropoma (Chondropomium) swiftii barahonense* Bartsch, 1946: Bartsch, 1946, pl. 4, fig. 3. *Chondropoma (Chondropomium) swiftii saturatum* Bartsch, 1946: Bartsch, 1946, pl. 4, fig. 4.

**Distribution:** Rift valley of Hoya de Enriquillo/Plain du Cul-de-Sac from the western shore of Étang Saumâtre, around Lago Enriquillo, east to Agua.

**Habitat:** Generally below 200 m under fossilized coral rubble and dead agave and grasses in xeric areas. Locally common.

**Other Material Examined:**

**“weinlandi form” (566 Specimens): Dominican Republic. Azua Province.** UF 216837(3), 3 km W of Hatillo; UF 45565(7), UF 45857(1), 12 km ESE of Las Charcas; UF 216805(1), UF 216833(1), 50 m, 8 km ESE of Las Charcas; UF 23180(7), 80 m, 2 km N of Las Charcas; UF 23162(11), 80 m, 2 km N of Las Charcas; UF 216834(62), 1 km N of Estebanía; UF 216830(83), 2 km SE of Azua; UF 216836(10), 3.5 km SSE of Azua; UF 216840(1), 25 km W of Azua; UF 45853(22), 70 m, 7 km E of Azua; UF 216839(1), 160 m, 15 km SW of Las Yayitas; UF 216827(9), 12 km E of Quita Coraza; OSUM 42361(32), 80 m, off road to Galindo Adrento, 2.8 km ESE of Galindo Adrento, 5.7 km WSW of Isura, 18.4062° N, –70.8909° W; UF 216809(16), 2 km NW of Cortés. **Peravia Province.** UF 216811(10), 20 m, 5 km N of Cruce de Ocoa. **Barahona Province.** UF 45584(4), 27 km W of Azua; UF 216835(7), 140 m, 14 km NE of La Canoa; GTW 7087b(2), Fondo Negro; UF 216824(25), 13 km ESE of La Canoa; UF 216828(6), Cerro de Sal, 2 km SW of Las Salinas; UF 216831(13), 9 km W of Cabral; UF 45644(9), 80 m, 1 km E of Las Salinas; GTW 7087c(1), OSUM 42365(13), 37 m, top of small hill, off road from Puerto Alejandro to La Canoa, 3.4 km NE of Bombita, 18.3482° N, –71.1225° W. **Independencia Province.** UF 45658(18), 80 m, 1 km WSW of Los

Saladillos; GTW 7087a(1), Mella; UF 216832(4), UF 249181(13); 1 km S of Mella; GTW 7087s(19), 42 m, along road to Angostura, 1 km NNW of Angostura, 18.3412° N, -71.4207° W; UF 45651(14), UF 45783(3), 60 m, 2 km NW of Angostura; UF 45684(13), 50 m, 3 km NW of Angostura; UF 216844(2), 250 m, 4 km SSE of Los Pinos del Eden; UF 216829(4), 2 km WNW of Postrer Río; UF 216826b(18), 7 km E of Las Descubierta; UF 45793(13), 17 km ESE of El Limón; UF 216848(26), 14 km WNW of Duverge; GTW 7087g(3), ridge NW of Jimaní, Independencia Province; GTW 7087d(5), S side of highway, a few km E of Jimaní, Independencia Province; OSUM 42379(7), Bartolomé, Independencia Province; OSUM 42377(2), 27 m, off RD 46, Independencia Province, 18.4167° N, -71.7075° W; OSUM 42378(31), 10 m, off RD 48, Independencia Province, 18.5204° N, -71.7614° W.

**“azuense form” (194 Specimens): Dominican Republic. Azua Province.** GTW 7087k(1), 191 m, top of small hill, off RD 2, 1.86 km ENE of Agua, 1.6 km W of Las Carreras, 18.3586° N, -70.5016° W; UF 45565(1), 12 km ESE of Las Charcas; UF 216837(2), 3 km W of Hatillo; UF 216823(6), 7 km SE of Hatillo; UF 216809(4), 2 km NW of Cortés; UF 216462(12), 3 km ESE of Cortés; UF 23180(2), 80 m, 2 km N of Las Charcas; UF 216805(4), 8 km SE of Las Charcas; UF 216834(20), 1 km N of Estebanía; UF 216866(7), 3 km SE of Azua; UF 216836(4), 3.5 km SSE of Azua. **Barahona Province.** GTW 7087p(4), 20 m, off road from Puerto Alejandro to La Canoa, 2.8 km NE of Bombita, 18.3478° N, -71.1298° W; OSUM 42364(5), 37 m, top of small hill, off road from Puerto Alejandro to La Canoa, 3.4 km NE of Bombita, 18.3482° N, -71.1225° W; UF 216846(27), 2 km NE of La Canoa; UF 216821(6), 3 km NE of La Canoa; UF 216454(5), UF 216847(1), 3 km ESE of La Canoa; UF 216822(15), 20 m, 12 km NE of La Canoa; UF 216831(1), 9 km W of Cabral; UF 45644(1), 1 km E of Las Salinas. **Independencia Province.** GTW 7087r(4), 42 m, quarried area along road to Angostura, 1 km NNW of Angostura, 18.3412° N, -71.4207° W; UF 45684(7), 60 m, 2 km NW of Angostura; UF 45684(7), 3 km NW of Angostura; GTW 7087w(5), semi-cleared pasture with piles of rocks, off RD 48, 18.5204° N, -71.7614° W; UF 45793(2), 17 km ESE of El Limón; UF 216832(4), 1 km S of Mella; OSUM 42359(19), Bartolomé; UF 216829(4), 2 km WNW of Postrer Río; GTW 7087f(15), Los Rios, N shore Lake Enriquillo.

**“barahonense/saturatum form” (421 Specimens): Dominican Republic. Azua Province.** UF 216823(20), 7 km SE of Hatillo; UF 216462(28), 3 km ESE of Cortés; UF 216809(3), 2 km NW of Cortés; GTW 7087m(1), 191 m, top of small hill, off RD 2, 1.86 km ENE of Agua, 1.6 km W of Las Carreras, 18.3586° N, -70.5016° W; UF 45565(34), UF 45857(11), 12 km ESE of Las Charcas; UF 216805(4), UF 216833(7), 50 m, 8 km SE of Las Charcas; UF 216834a(9), 1 km N of Estebanía; UF 216827(9), Monte Río; UF 216836(9), 3.5 km SSE of Azua; UF 216830(1), 12 km E of Quita Coraza. **Barahona**

**Province.** UF 45589(2), 270 m, 9 km NE of La Canoa; UF 216838(3), 170 m, 9 km NE of Fondo Negro; UF 467518(6), 1.6 km W of Fondo Negro; GTW 7087x(5), 20 m, off road from Puerto Alejandro to La Canoa, 2.8 km NE of Bombita, 18.3478° N, -71.1298° W; OSUM 42363(3), 37 m, top of small hill, off road from Puerto Alejandro to La Canoa, 3.4 km NE of Bombita, 18.3482° N, -71.1225° W; OSUM 42362(20), 20 m, off road from Puerto Alejandro to La Canoa, 2.8 km NE of Bombita, 18.3478° N, -71.1298° W; UF 216846(9), 2 km NE of La Canoa; UF 216821(11), 3 km NE of La Canoa; UF 216847(51), 3 km ESE of La Canoa; UF 216824(5), 13 km ESE of La Canoa; UF 216822(68), 12 km NE of La Canoa; UF 216831(13), 9 km W of Cabral; UF 45644(2), 1 km E of Las Salinas; UF 45633(3), 3 km E of Las Salinas. **Independencia Province.** UF 45651(7), UF 45684(3), 60 m, 2 km NW of Angostura; UF 45684(3), 3 km NW of Angostura; UF 45661(3), 5 km W of Los Saladillos; UF 216832(31), 1 km S of Mella; UF 45658(8), 80 m, 1 km SSW of Los Salidillos; UF 216829(8), 2 km WNW of Postrer Río; UF 216817(1), 150 m, 6 km NW of Postrer Río; UF 216842(2), 10 m, 4 km E of La Descubierta; UF 216843(3), 100 m, 3 km NNE of La Descubierta.

**Variation Among Specimens:** See under “Remarks” below.

**Comparison With Other Species:** The unexpanded lip differentiates this species from *S. superbum* and *S. asymmetricum*. *Chondropomium beatense*, *C. blaineorum*, and *C. lynx* are similar but occur on the opposite slopes of the Sierra Baoruco. In addition, *C. blaineorum* and *C. lynx* have color patterns not seen in the nearly 1100 specimens of *C. weinlandi* examined. *Chondropomium blaineorum* has a peculiar mosaic pattern whereas *C. lynx* has smeared individual spots. Some specimens of *C. beatense* in particular resemble the *barahonense* form of *C. weinlandi* (but is geographically the farthest away from that species); they have a shorter, more conic, less inflated shell than does *C. weinlandi*. *Chondropomium sardonix* is sympatric with most of the *C. weinlandi* color forms but the striking orange and black two-tone color pattern is unique to it.

Dead specimens of *Crossepoma vermiculatum* Bartsch, 1946 lacking an operculum are very similar to the “azuense form” and are sympatric. That species has a unique underlying pattern of vertical grey markings and regular sutural spots not found in the “azuense form”. *Crossepoma vermiculatum* has a pseudolamella.

**Remarks:** Three groups of similar shells may be recognized based on color pattern. Bartsch (1946), as “*Chondropoma swiftii*,” described them as five subspecies. (However, as explained below, this species is not *Cyclostoma swiftii* Shuttleworth, 1854.) Pfeiffer (1862) had referred to his 1854b, pl. 37, figs. 1 and 2 and his 1854d, pl. 49, figs. 17–20 all as variants of *C. weinlandi*. Bartsch (1946) separated Pfeiffer’s pl. 49, fig. 19 as an

example of *C. vermiculatum* Bartsch, 1946, relegating his remaining figures to various subspecies of *C. "swiftii"*.

Bartsch's breakdown was:

1) "*swiftii swiftii*": Narrow interrupted spiral brown bands on a "buff" background (Figure 59). This is the least common of the forms.

2) "*swiftii weinlandi*": Narrow interrupted spiral brown bands on a "flesh-colored" background (Figures 51–58). The differences in background color do not seem significant and the *swiftii* and the "*weinlandi* forms" are here considered the same. This is the most common variant.

3) "*swiftii saturatum*": Broad, more or less continuous brown bands, which may appear as adjacent blotches (Figure 65).

4) "*swiftii barahonense*": Narrower continuous brown bands. Based on the material studied here, the *saturatum* and *barahonense* morphs cannot be differentiated (Figures 63, 64, 66).

5) "*swiftii azuense*": Bands absent or nearly so, background white (Figures 69–72).

Bartsch, working with a very small sample size, saw not only differences in color but differences in ranges, with the subspecies being allopatrically distributed. However, subsequent, more intensive collecting clearly demonstrates that these forms are not allopatric. All generally overlap (Figure 185) and are widely distributed in the rift valley of Hoya de Enriquillo/Plain du Cul-de-Sac where all three forms may be found under the same rock. Although the three forms cannot be subspecies, they are (usually) separable. What is their relationship to each other and are they distinct species or a polymorphic species for color?

In our phylogenetic analysis all three morphs formed a single monophyletic clade. However, the color forms did not segregate together (Figure 5). Neither was there any apparent geographic pattern. We conclude that *C. weinlandi* does not consist of phylogenetically separable units based on color forms but rather represents co-occurring polymorphic morphotypes.

Differences in shell color may extend to animal color as well. In the "*weinlandi* color form" the animal is pale tan with grey mottling between the eyes and on the snout and the tentacles. In the "*azuense* color form" the entire animal, including the tentacles, is a uniform pale tan, slightly darker on the foot, lacking the grey coloration; this might be considered a leucistic phenotype. The animal of the "*barahonense* color form" has not been recorded.

The taxonomic history of *C. weinlandi* is unusually complicated, beginning with Lamarck, entwining the taxonomy of several nominal species. In 1822, Lamarck described but did not illustrate *Cyclostoma semilabris* from a unknown locality; neither did he refer to any published figure. He described its sculpture as "*minutissime cancellata*." Pfeiffer (1862) proposed that it originated from the Bahamas. Bartsch (1946) did not concur with Pfeiffer and identified Lamarck's species as a Hispaniolan taxon. In 1952, Mermod figured (his figure 109) the type of *Cyclostoma semilabris* in the Muséum d'histoire naturelle de Genève (unnumbered). This specimen proved to be different from Bartsch's

Hispaniolan species but very similar to several Bahamian/Caicos taxa, especially *Chondropoma ljahmarsoni* Pfeiffer, 1858, from Turks and Caicos. This left Bartsch's Haitian species without a valid name, which prompted it to be described as *Chondropoma bellevittatum* Watters, 2016a.

Shuttleworth (1854) described but did not illustrate *Cyclostoma swiftii*. He stated that it was collected from Ponce, southern Puerto Rico, by Swift and had been in the collection of Bland. Indeed, Dall and Simpson (1901) and Baker (1941) listed this species from Puerto Rico and were followed in this identification by van der Schalie (1948), who illustrated a specimen as *C. swiftii* from Ponce. However, that shell bears no resemblance to the species complex discussed here from Hispaniola. This Ponce taxon was later described as *Chondropoma schaliei* Baker, 1950; Baker did not comment on why he discarded *C. swiftii* in favor of the new species name. Shuttleworth, in the description of *C. swiftii*, mentioned "*obtuse decussata*," a sculpture not found in the Hispaniolan species complex discussed here. He compared *C. swiftii* to his Puerto Rican *Cyclostoma blauneri* Shuttleworth, 1854, also having decussate sculpture.

Apparently based solely on Lamarck's brief description of his "jolie coquille," Sowerby (1843: pl. 24, fig. 60) illustrated a specimen supposedly from Cuba as Lamarck's *C. semilabris*. Like Shuttleworth's description of *C. swiftii* and Lamarck's description of *C. semilabris*, Sowerby's illustration and description also indicated a cancellate sculpture. The Hispaniolan species complex described here lacks such sculpture and that complex would appear to be neither *C. swiftii* nor *C. semilabris*.

Later, Pfeiffer (1852a) redescribed his "*Chondropoma semilabre* Lamarck," giving Haiti as the provenance rather than the Bahamas, Puerto Rico, or Cuba. He added that Sallé had collected the specimen(s). As Sallé only collected in the Dominican Republic portion of Hispaniola, Pfeiffer's use of "Haiti" referred to the entire island. However, Pfeiffer described the species (p. 286) as having "*lineis spiralibus obsoletissimis interdum decussatula*," which, again, is a sculpture lacking in the Hispaniolan taxa. But in 1862 he retracted this line of description as inapplicable stating that he had copied it, apparently inadvertently, from Lamarck's original description. Clearly, whatever their valid name, by this time Pfeiffer was working with specimens in the Hispaniolan species complex described here.

In 1862, Pfeiffer had again changed his mind concerning the identification of *C. semilabris*. In 1854 Pfeiffer had figured his Hispaniolan specimens of "*C. semilabris*" (1854b, pl. 37, figs. 1 and 2 and 1854d, pl. 49, figs. 17–20). These shells undoubtedly belong to the species complex recognized here and not to any Bahamian, Cuban, or Puerto Rican species. By 1862, Pfeiffer had come to believe they were not Lamarck's *C. semilabris*, which Pfeiffer now believed was a Bahamian species. Neither did he include *C. swiftii* in his deliberations, apparently dismissed as a Puerto Rican taxon and not under consideration for this Hispaniolan species. In his mind this left the Hispaniolan species without a valid name. He

named it *Chondropoma weinlandi* Pfeiffer, 1862, from “Haiti” referring back to his 1854b and 1854d figures of “*C. semilabris*.” Reeve (1863c) figured it as well under *C. weinlandi*.

The description of decussate sculpture in the original description of *C. swiftii*, and the subsequent mention of such sculpture by Sowerby, suggest that Shuttleworth’s species is not the Hispaniolan species, i.e., the “*C. swiftii*” of Bartsch. Mermod (1952) mentioned, but did not illustrate, the type of *C. swiftii* in the Naturhistorische Museum, Bern. He compared it with presumed specimens of *C. semilabris* and pronounced that they were the same species. Swift himself either collected or employed someone else to collect in Puerto Rico (Clench, 1938), but is not listed by Bartsch (1946) as having collected in Hispaniola. How then did *C. swiftii* come to be associated with Hispaniola?

The key point occurred when Bartsch (1946) figured the stated type of *C. swiftii*, which matched the Hispaniolan species complex studied here, but lacked the decussate sculpture described by Shuttleworth. Bartsch recognized *C. weinlandi* as a subspecies of *C. swiftii* differing only in the background color of the shell. He further separated Pfeiffer’s 1854b and 1854d figures into several subspecies of *swiftii* and renamed the 1854d figure 19 as *Chondropoma vermiculatum* Bartsch, 1946. This might have ended the confusion surrounding the identity of *C. swiftii*, although leaving some nagging questions unanswered concerning sculpture and the fact that Swift may never have collected in Hispaniola.

In preparation of this study, we contacted E. Neubert at the Naturhistorische Museum, Bern, for a digital photograph of the type of *C. swiftii*. The photograph of the specimen sent to us is not only not the same specimen as figured by Bartsch but represents a different species entirely: *Chondropoma pictum* Pfeiffer, 1839, from Cuba. This same specimen was also illustrated as one of the syntypes (NMBE 19109/4) for *C. swiftii* by Neubert and Gosteli (2005: pl. 15, fig. 1). It should be noted that *C. pictum* has predominantly spiral threads with irregular axial growth marks that could be construed as decussate sculpture. Specimens may also be colored as described by Shuttleworth for *C. swiftii*, particularly the subspecies or “color form” *C. p. celsum* Torre and Bartsch, 1938. Shuttleworth indicated that his specimen of *C. swiftii* had been sent to him by Bland. Bland possessed a large collection of land snails from the Caribbean, including Cuba, and it is possible that Bland had inadvertently switched a label from Cuba for that of Puerto Rico. But it is unclear if Swift ever collected in Cuba.

Several explanations are possible. Perhaps the specimen shown to us was part of a syntype lot that may consist of mixed species, of which a different specimen and species was the one figured by Bartsch. However, E. Neubert (pers. comm., 2015), upon examination stated that none of the specimens match that shown by Bartsch and all appear to be *C. pictum*. Was it possible that Bartsch never returned the specimen? Bartsch stated (1946: 28): “Through the kindness of the Naturhistorische

Museum at Berne, Switzerland, I have been able to examine and figure the type.” But did Bartsch have the specimen in hand? His figure of it, plate 4, figure 2, seems of a different quality than all of his other figures: it is slightly out of focus, appears washed out, and is oriented slightly differently. It appears to be a photograph of a photograph, suggesting he did not have the specimen in hand but only a photograph supplied by the Bern museum. Furthermore, Mermod (1952) said “I was able, thanks to Professor Baumann, the Museum of Bern, to compare *swiftii* types of Shuttleworth and his named *semilabris* examples” [from the French] indicating that the types were back in Bern by 1952, although perhaps still missing Bartsch’s possible loan. None of these scenarios would seem to explain the discrepancy.

In summary: 1) the specimen illustrated as the type of *C. swiftii* by Bartsch does not match any of the existing syntypes; and 2) Shuttleworth’s description of *C. swiftii* does not match the Hispaniolan species of Bartsch. The question of where Bartsch’s specimen originated (and where it went) remains a mystery. But based on the evidence presented here *C. swiftii* is not the Hispaniolan species and the earliest available name is *Chondropoma weinlandi* Pfeiffer, 1862. The existing syntypes of *C. swiftii* are specimens of the Cuban *Cyclostoma pictum*, and *C. swiftii* is a junior synonym of that name. However, the types of *C. swiftii* are very similar to *C. pictum celsum* Torre and Bartsch, 1938, and may represent an earlier name for that subspecies.

Weinland (1880) listed two varieties, both unfigured and undescribed, from “St. Domingo:” *Chondropoma weinland* var. *major* (p. 346) and *Chondropoma weinlandi* var. *malleata* (pp. 343, 346). They are *nomina dubia*.

**Original Description:** *Chondropoma weinlandi* Pfeiffer, 1862. Pfeiffer’s 1852a description of “*Ch. semilabre* Lamarck” appears to be the earliest description of *C. weinlandi*, although apparently conflating the two species. From the Latin. “Shell subumbilicate, ovate-elongate, truncate, somewhat solid, longitudinally plicate, very obsolete spiral lines sometimes decussate, shiny, diaphanous, white, ornated with interrupted lines perhaps narrow and numerous brown bands; suture very minutely crenulated; 4 remaining whorls a little convex, the front of the last a little solute, the top carinate, base concentrically striate; aperture vertical, obliquely acuminate-ovate; peristome obtuse, everywhere narrowly expanded. Operculum white.” In 1862, he removed the phrase “very obsolete spiral lines sometimes decussate” from the description, which he had based on Lamarck’s description.

**Etymology:** *Chondropoma weinlandi* Pfeiffer, 1862: Cristoph David Frederick Weinland (1829–1914), German/American conchologist, physician. *Chondropoma* (*Chondropomium*) *swiftii azuense* Bartsch, 1946: Azua, Dominican Republic. *Chondropoma* (*Chondropomium*) *swiftii barahonense* Bartsch, 1946: Barahona, Dominican Republic. *Chondropoma* (*Chondropomium*) *swiftii saturatum* Bartsch, 1946: L. *saturatus*, fill, glut; perhaps “filled” with dark color.

Genus *Chondropomella* Bartsch, 1932

**Type Species:** *Cyclostoma magnificum* Pfeiffer, 1852, by original designation.

**Description:** Shells very large for family (to ca. 32 mm length), turbinoid rather than elongate, usually decollate. Protoconch of 1.5 smooth, minute whorls. Final whorl barely detached for short distance from previous whorl. Axial sculpture of wide, flattened, close-set ribs. Spiral sculpture absent except for threads in umbilicus. Overall sculpture very smooth, often polished. Suture serrate but lacks fused tufts. Adult shell with reflected lip. Lip double, inner lip usually erect and separate from outer lip. Outer lip broadly expanded but narrowest facing umbilicus; adnate or very narrowly separated from previous whorl. Color pattern of spiral bands and blotches, continuous or interrupted; pattern unknown in *Chondropomella platychilum*. Operculum only known for *C. magnificum*: paucispiral with pseudolamella occupying inner proximal half of each opercular whorl, outer half with erect lamellae oriented along growth lines. Radula known only from *C. magnificum*: inner marginal tooth of radula broadly triangular, long side being proximal, with irregular coarse serrations, lacking denticle on lateral side. Animal as in *Chondropomium*.

**Remarks:** *Chondropomella* was introduced as *Chondropomella* on p. 2, but spelled *Chondropomella* in all other instances. Watters and Duffy (2010) placed *Chondropoma asymmetricum* Pilsbry, 1922, and *Chondropoma inaequilabrum* Bartsch, 1946, in *Chondropomella*. These two are here shown to be synonymous and to belong to the new, distinctive genus *Superbipoma*, based on phylogenetic, radular, and conchological evidence.

When Bartsch named *Chondropomella* (1946) he was unaware of the operculum of either of the two species that he placed in the genus. Pfeiffer (1854a) described a chondropomine operculum for *Chondropoma magnificum* Pfeiffer, 1852, which nevertheless appears pseudolamellate a subsequent publication of his (Pfeiffer, 1854a: fig. 3).

*Chondropomella* is known from three rare species. *Chondropomella magnifica* is the most common but still rare outside of a few collections; *C. platychilum* is only known from a handful of worn shells, and *C. virilis* is known from two collections of unknown provenance. The habitat is only known for *C. magnifica*. Like *Chondropomium*, it lives in very xeric limestone foothills with sparse vegetation. Genetic material was only available for *C. magnifica*, apparently the only species of the genus that has been collected alive.

*Chondropomella magnifica* (Pfeiffer, 1852)

(Figures 74–88, 183)

## CHRESONYMY

*Chondropoma magnificum* “Salle” Pfeiffer, 1852a: 278–279; Pfeiffer, 1853a: 197; Pfeiffer, 1854c: pl. 47, figs. 20–22; Pfeiffer, 1854d: 365–366; Pfeiffer, 1858b: 136.

*Cyclostoma (Chondropoma) magnificum* “Salle” Pfeiffer, 1852: Pfeiffer, 1854a: 142, pl. 13, figs. 3a–c.

*Cyclostoma magnificum* Pfeiffer, 1852: Pfeiffer, 1854c: pl. 47, figs. 20–22; Pfeiffer, 1854d: 365–366.

*Chondropoma magnificum* “Salle”: Adams and Adams, 1856: 295; Chenu, 1859: 493, fig. 3650; Bland, 1861: 355; Pfeiffer, 1865: 145; Pfeiffer, 1876: 190; Kobelt, 1879: 198; Tryon, 1883: 284, pl. 76, fig. 82; Crosse, 1891: 170.

*Chondropoma magnifica* (Pfeiffer, 1852): Reeve, 1863: pl. 1, figs. 1b,c [not 1a, see below].

*Chondropoma (Chondropomium) magnifica* (Pfeiffer, 1852): Henderson and Bartsch, 1920: 60.

*Chondropoma (Chondropomella) magnifica* (“Salle” Pfeiffer, 1852): Bartsch, 1932: 3.

*Chondropoma (Chondropomella) magnificum* (Pfeiffer, 1852): Bartsch, 1946: 38–39, pl. 8, fig. 7.

*Chondropomella magnifica* (Pfeiffer, 1852): Watters, 2006: 59, 60, 341–342.

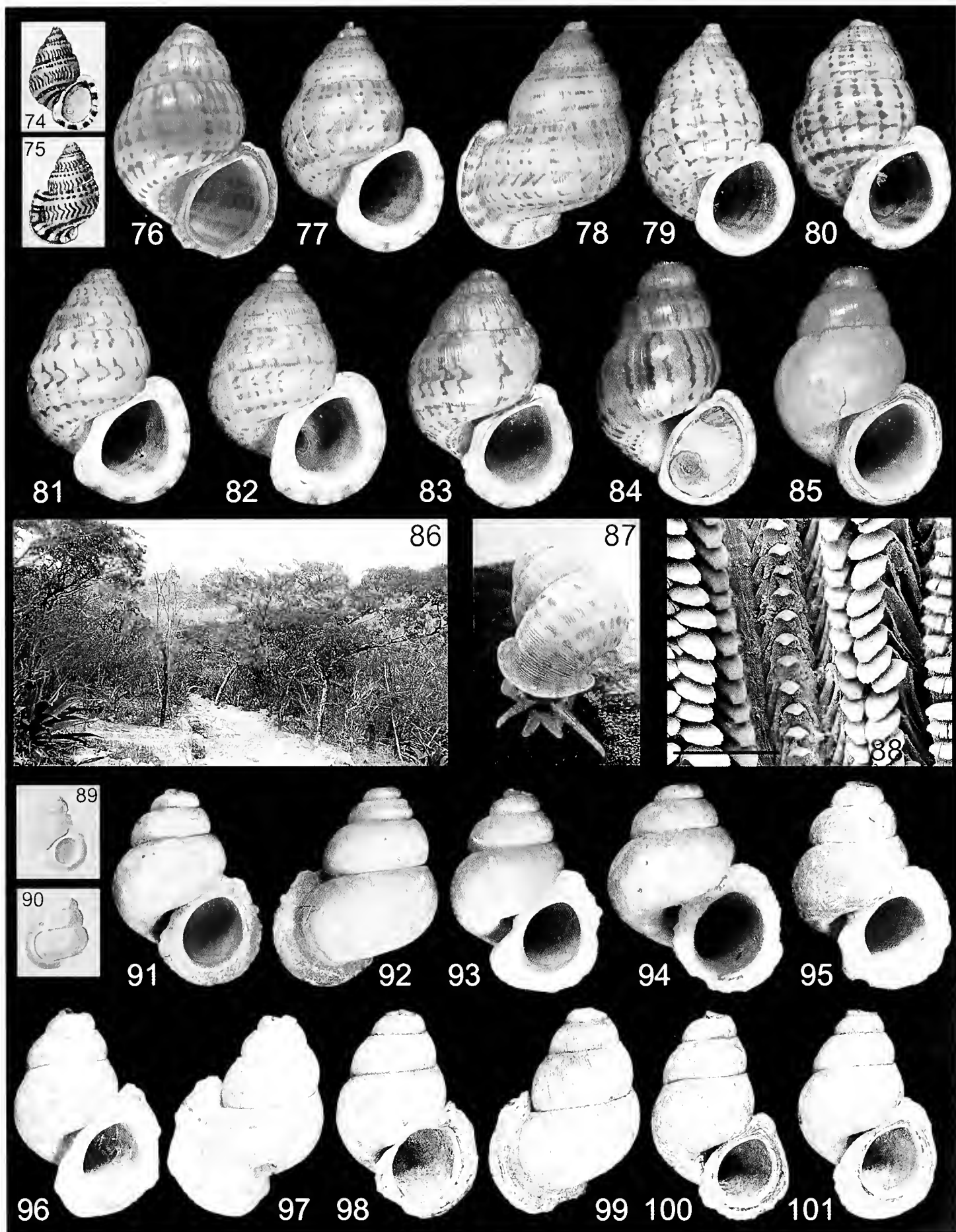
*Chondropomella elegans* Watters and Duffy, 2010: 10–11, figs. 32–36.

*Chondropomella magnificum* [sic] (Pfeiffer, 1854): Watters and Duffy, 2010: 10, 11, fig. 31.

*non Chondropoma magnificum* var. Reeve, 1863: pl. 1, fig. 1a [= *Cyclostoma gutierrezii* “Poey” Pfeiffer, 1858a, *vide* Arango y Molina, 1878: 32 and Crosse, 1890: 296].

**Description:** Shell very large for family (largest adult specimen 31.5 mm maximum length, decollate, including peristome; smallest adult specimen 22.7 mm length, decollate, including peristome), solid, polished, conic, umbilicus minute. Protoconch of 1.5 white, smooth whorls. Adult specimens usually decollate. Teleoconch of 4–5.5 whorls, final whorl adnate or detached for last 1/6th of whorl. Suture indented, shallowly channeled. Peristome double, tear drop-shaped. Outer lip thickened, composed of numerous lamellae, rolled back abaperturally, undulating, folded over umbilicus, narrowest facing umbilicus, adnate or very narrowly detached from previous whorl, auriculate posteriorly. Inner lip adherent to outer lip or barely exerted. Spiral sculpture present only as 4–5 very feeble cords within umbilicus. Axial sculpture of numerous (160–170) narrow, widely spaced, very low undulating ribs, forming minute serrations at suture. Background color white to tan with broken spiral bands of spots and chevrons; bands extend onto face of outer lip but not onto inner lip. Operculum with thick pseudolamella divided into two regions: outer half of spiral with very coarse erect lamellae, inner half fused into smooth plate. Radula as in genus. Animal tan to yellowish with dark brown band between eyes and across base of snout.

**Type Material:** *Chondropoma magnificum* Pfeiffer, 1852: ? Syntypes (3): NHMUK. Three specimens glued to a board at NHMUK, unnumbered, of “*magnificum* var. W. Indies” from Cuming collection; back of board reads “No. 132, *Cycl. magnificans* var. Salle. St. Domingo.” These may be syntypes but do not match Pfeiffer (1854a: pl. 13, figs. 3a, b). They are not *Chondropoma magnificum*.



**Figures 74–101.** *Chondropomella* species. **74–88.** *Chondropomella magnaifica* (Pfeiffer, 1852). **74, 75.** Pfeiffer, 1854a, pl. 13, figs. 3a,b. **76.** *Chondropomella elegans* Watters and Duffy, 2010. UF 420732, holotype, 27.2 mm. **77, 78.** UF 216670b, 26.4 mm. **79.** UF 216387, 23.2 mm. **80.** UF 216387, 22.7 mm. **81.** UF 216671, 26.2 mm. **82.** UF 216671, 24.8 mm. **83.** GTW 7639a, 26.1 mm. **84.** OSUM 42368, 28.6 mm. **85.** UF 217950, 27.5 mm. **86.** Habitat. **87.** Living individual. **88.** OSUM 42368, radula. Scale bar = 200  $\mu$ m. **89–95.** *Chondropomella platychihum* (Pfeiffer, 1851). **89, 90.** *Cyclostoma latilabre* “d’Orbigny” of Pfeiffer, 1847: pl. 10, figs. 26, 27. **91, 92.** UF 216766, 29.6 mm. **93.** UF 216767, 26.3 mm. **94.** UF 216768, 24.3 mm. **95.** USNM 354984, 28.6 mm. **96–101.** *Chondropomella virilis* (Bartsch, 1946). **96, 97.** USNM 504145, holotype, 18.7 mm. **98, 99.** USNM 425379, 21.8 mm. **100.** USNM 425379, 13.4 mm. **101.** USNM 425379, 18.5 mm.

var. Reeve, 1863. *Chondropomella elegans* Watters and Duffy, 2010: Holotype: UF 420732; Paratype: OSUM 32485(1); NHMUK 199349(1).

**Type Locality:** *Chondropoma magnificum* Pfeiffer, 1852: "Habitat in insula Haiti" ["Rocks at the entrance of a cave at Barrera, Dominican Republic" [from the French], *vide* Crosse, 1890.] ["This locality is in the Province of Azua about 16 miles southwest of the town of Azua," *vide* Bartsch, 1946]. *Chondropomella elegans* Watters and Duffy, 2010: "Dominican Republic, Independencia Province, ~ 8 km SW of Duvergé, Puerto Escondida."

**Type Figured:** *Chondropoma magnificum* Pfeiffer, 1852: Pfeiffer, 1854a, pl. 13, figs. 3a–c. *Chondropomella elegans* Watters and Duffy, 2010: Watters and Duffy, 2010, figs. 32, 33.

**Distribution:** Along the slopes facing Lago Enriquillo from the northwest shore along the southern shore to the isolated Sierra Martín García and the lowlands surrounding the Bahía de Ocoa. Locally common.

**Habitat:** Hillsides under fossilized coralline blocks in open xeric areas with sparse vegetation. It has also been observed suspending itself from short mucus threads from rocks.

**Other Material Examined (517 Specimens): Dominican Republic. Independencia Province.** OSUM 42358(16), Bartolomé; UF 216850a(15), 7 km SE of Jimaní; GTW 16031e(3), ca. 0.8 km from Puerto Escondido, S of Duvergé; UF 217956(17), 520 m, 3 km SE of Puerto Escondido; UF 217950(27), UF 217950a(12), 830 m, 4 km ESE of Puerto Escondido; UF 35087(1), 7.5 km S of Puerto Escondido; UF 217960(4), 8 km WNW of Puerto Escondido; UF 217954(1), 490 m, 11 km WNW of Puerto Escondido; UF 217953(6), UF 217959(6), 2 km SW of Duvergé; UF 217951(12), UF 217955(12), UF 217957(20), 9 km WNW of Duvergé; UF 217982(2), 12 km WNW of Duvergé; OSUM 42368(17), 466 m, on footpath up hill, 1.3 km E of center of Puerto Escondido, 18.3290° N, -71.5593° W; GTW 16031e(1), 42 m, quarried area along road to Angostura, 1 km NNW of Angostura, 18.3412° N, -71.4207° W; GTW 16031d(3), 473 m, along RD 541, 2.3 km NNW of El Naranjo, 18.3514° N, -71.6279° W; UF 45679(3), 2 km E 2 km S of Angostura; UF 45669(3), 1 km E 2 km S of Angostura. **Azua Province.** GTW 7639a(1), 244 m, on trail at Barrera; UF 216669(30), UF 216673(2), 150 m, Barrera; UF 216670b(39), UF 216671(37), 160 m, Barrera; UF 216769(1), 560 m, Sierra Martín García, 5 km NNW of Barrera; UF 216674(1), W slope of Loma del Aguacate; UF 216387(163), 80 m, 7 km E of Azua; UF 216506(2), UF 216521(10), UF 216522(16), UF 216523(21), Sierra El Numbrero, 8 km SE of Las Charcas; UF 46258(1), UF 216524(2), 100 m, 12 km ESE of Las Charcas; UF 216520(24), UF 216519(21), 3 km W of Hatillo. **Barahona Province.** UF 216672(4), 3 km NE of Puerto Alejandro.

**Variation Among Specimens:** Specimens differ in the degree of coloration and the degree of expansion of the lip. Rare specimens may be without any color pattern.

**Comparison With Other Species:** The lip may be barely adnate to the previous whorl in this species but it is broadly fused in *C. platyichilum* and *C. virilis*. *Chondropomella platyichilum* has a shorter spire and more rounded whorls than the other species. *Chondropomella virilis* differs from the other species in having a white shell with a few spiral brown bands that extend over the greatly expanded lip and a coarser sculpture of raised narrow lamellae rather than flattened ribs.

**Remarks:** *Chondropoma magnificum* was recognized by Bartsch (1946) as the population from the isolated Sierra Martín García having a wide, wholly adnate outer lip. *Chondropomella elegans* was differentiated as the western population in the Lago Enriquillo rift valley having a narrower, solute outer lip. A third population occurs around the Bahía de Ocoa that resembles *C. elegans*. Examination of over 500 specimens suggests the variation in shell morphology within a population is as great as that between populations and the three are considered a single taxon pending further genetic studies.

**Original Description:** Pfeiffer, 1852a: 278–279. From the Latin. "Shell umbilicate, ovate-conic, thin, longitudinally plicate-striated, diaphanous, a little shining, white, variously interrupted brown bands, middle widest from angular striped shapes, ornate; spire inflated, apex subtruncate; suture simple; remaining 5 whorls a little convex; last one rounded; aperture vertical, oval; peristome simple, shining, white, brown-spotted, top with expanded hood, narrowly adnate to previous whorl, narrow, sinuate at the umbilicus, then broadened into a open tongue, right margin and base wide reflexed arching. Operculum cartilaginous, flat, pale corneous."

**Etymology:** *Chondropoma magnificum* Pfeiffer, 1852: *L. magnificus*, magnificent. *Chondropomella elegans* Watters and Duffy, 2010: *L. elegans*, elegant.

### *Chondropomella platyichilum* (Pfeiffer, 1851) (Figures 89–95, 183)

#### CHRESOONYMY

*Cyclostoma latilabre* "d'Orbigny" Pfeiffer, 1847: 78–79, pl. 10, figs. 26, 27 [misidentification, *non Cyclostoma latilabris* d'Orbigny, 1842]; Pfeiffer, 1851: 169 [in synonymy of *Cyclostoma platyichilum* Pfeiffer, 1851]; Pfeiffer, 1852a: 261, 294 [in synonymy of *Cyclostoma platyichilum* Pfeiffer, 1851]; Pfeiffer, 1852b: 41 [in synonymy of *Cyclostoma platyichilum* Pfeiffer, 1851]; Bartsch, 1946: 37 [in synonymy of *Cyclostoma platyichilum* Pfeiffer, 1851].

*Cistula? platyichila* Pfeiffer, 1851: 169; Pfeiffer, 1852a: 261; Pfeiffer, 1852b: 41; Pfeiffer, 1853a: 182; Pfeiffer, 1858b: 130; Pfeiffer, 1865: 140; Pfeiffer, 1876: 187.

*Cyclostoma platychilum* (Pfeiffer, 1851): Pfeiffer, 1853b: 266; Pfeiffer, 1858b: 130.

*Cistula platychila* (Pfeiffer, 1851): Adams and Adams, 1856: 294.

*Cistula platychila*? (Pfeiffer, 1851): Arango y Molina, 1878: 31.

*Chondropoma* (*Chondropomella*) *platychilum* (Pfeiffer, 1851): Bartsch, 1946: 37, pl. 7, fig. 1.

*Chondropomella platychila* [sic] (Pfeiffer, 1851): Watters, 2006: 60, 410–411.

*Chondropomella platychilum* (Pfeiffer, 1851): Watters and Duffy, 2010: 10, 11.

*non* ?*Cistula platychila* “Pfeiffer” Arango y Molina, 1878: 31 [= *Cyclostoma latilabris* d’Orbigny, 1842, *vide* Bartsch, 1946: 37].

**Description:** Shell very large for family (largest adult specimen 29.6 mm maximum length, decollate, including peristome; smallest adult specimen 24.3 mm length, decollate, including peristome), solid, low-spired, umbilicus wide. Protoconch decollated from all examples. Adult specimens decollate. Teleoconch of 3.5 whorls, final whorl barely detached for last 1/6th of whorl. Suture indented, shallowly channeled. Peristome double, oval. Outer lip thickened, widely expanded, composed of numerous lamellae, rolled back abaperturally, undulating, folded over umbilicus, narrowest facing umbilicus, broadly adnate with previous whorl, widely auriculate posteriorly and at 8 o’clock position. Inner lip narrowly erect. Axial sculpture absent but perhaps worn away in all specimens. Spiral sculpture of few weak threads in umbilicus. Suture smooth. All specimen worn and faded with no indication of color patterns. Operculum, anatomy, and radula unknown.

**Type Material:** Not located. On his death, many of Pfeiffer’s specimens passed to Heinrich Dohrn (1838–1913). Dohrn’s collection was incorporated into the Museum Narodone in Szczecin, Poland. Although some of the other collections of that museum were moved to the Pommerisches Landesmuseum, Greifswald, Germany, the natural history collections are not there (pers. comm., B. Frenssen, 2016). Dohrn’s collection, and Pfeiffer’s types, were probably destroyed by Allied bombing of the Museum Narodone in WW II.

**Type Locality:** “Cuba,” for *Cyclostoma latilabre* “d’Orbigny” of Pfeiffer, 1846. *Cistula*? *platychila* Pfeiffer, 1851: “Habitat...?” Here restricted to 8 km NW of Oviedo, Pedernales Province, Dominican Republic.

**Type Figured:** Pfeiffer, 1847, pl. 10, figs. 26, 27?

**Distribution:** All records are for the Oviedo region in the southern Sierra Baoruco foothills, one record around the Lago de Oviedo.

**Habitat:** This species is very rare in collections. It is likely that its exact habitat has not been discovered.

**Other Material Examined (5 Specimens): Dominican Republic. Pedernales Province.** UF 216768(1), 8 km NW of Oviedo; UF 216767(1), along shore of Lago de Oviedo, 1 km SE of Oviedo Viejo; UF 216756(1), 210 m, 17 km NW of Oviedo; USNM 354984(2), Trujin [Lago de Oviedo].

**Variation Among Specimens:** The few known specimens are remarkably uniform in shell characteristics.

**Comparison With Other Species:** See under *C. magnificum*.

**Remarks:** This is one of the largest species in the family – to ca. 30 mm length. Pfeiffer seems to have had a fresh specimen before him but all other shells known to us are weathered and faded. The color pattern, if any, is unknown and Pfeiffer only described it as “diaphanous, hyaline-white.” No material was available for phylogenetic study.

**Original Description:** *Cyclostoma latilabre* “d’Orbigny” Pfeiffer, 1847: 78–79. From the Latin. “Shell umbilicate, ovate-oblong, decollate, a little thin, smooth, diaphanous, hyaline-white; 4 convex whorls, base of last spirally and obsoletely subsulcate; aperture vertical, oval; peristome double, inner subexpanded, hardly prominent, external slightly thickened, angle widely reflexed, bordered to the penultimate whorl with thick narrow angulate junction columella expanded in middle angle.”

**Etymology:** *G. platys*, broad + *G. cheilos*, mouth. A noun in apposition.

### ***Chondropomella virilis* (Bartsch, 1946)**

(Figures 96–101)

CHRESOXYMY

*Incertipoma virile* Bartsch, 1946: 171, 174–175, pl. 30, fig. 8.

*Chondropomella virilis* (Bartsch, 1946): Watters, 2006: 60, 547.

*Chondropomella virile* [sic] (Bartsch, 1946): Watters and Duffy, 2010: 10, 11.

**Description:** Shell medium to large for family (largest adult specimen 21.8 mm maximum length, decollate, including peristome; smallest adult specimen 13.4 mm length, decollate, including peristome), solid, low-spired, umbilicus wide. Protoconch decollated from all examples. Adult specimens decollate. Teleoconch of 3.5 whorls, final whorl almost completely adnate with previous whorl. Suture indented, channeled. Peristome double, oval. Outer lip thickened, widely expanded, composed of numerous lamellae, rolled back abaperturally, undulating, folded over umbilicus, narrowest facing umbilicus, weakly adnate with previous whorl, widely auriculate posteriorly and at 8 o’clock position. Inner lip narrowly erect. Axial sculpture of ca. 110–120 narrow, erect, widely spaced lamellae. Spiral sculpture of ca. 3 cords in umbilicus.

Suture smooth. The holotype has vestiges of color pattern but all other specimens are worn and faded. The holotype has 9 nearly continuous, narrow, spiral tan bands between suture and base; bands extend onto abapertural face of outer lip but only faintly onto adapertural side. Operculum, anatomy, and radula unknown.

**Type Material:** Holotype: USNM 504145.

**Type Locality:** "Haiti."

**Type Figured:** Bartsch, 1946, pl. 30, fig. 8.

**Distribution:** Unknown. The two lots of this species are stated to come from "Haiti" but it is not clear if this refers to the country of Haiti or the island of Hispaniola. We expect that, like other members of the genus, it is endemic to the Barahona Peninsula awaiting rediscovery.

**Habitat:** Not recorded.

**Other Material Examined (24 specimens):** "Haiti." USNM 504145(1); USNM 425379(23), "probably Haiti."

**Variation Among Specimens:** The few known specimens vary in the degree of expansion of the lip.

**Comparison with Other Species:** See under *C. magnifica*. The lamellate sculpture on the whorls is unique.

**Remarks:** This rare, distinctive species, like *C. platychilum*, is known mainly from worn specimens. The lamellate sculpture is unlike other *Chondropomella* and discovery of specimens with opercula (or live ones with genetic material) may necessitate reallocation to a different genus. It bears some resemblance to members of *Sallepoma* from the western Tiburon peninsula.

**Etymology:** *L. virilis*, manly.

### Genus *Clydonopoma* Pilsbry, 1933

**Type Species:** *Tudora nobilis* Pfeiffer, 1852, by original designation.

*Parachondria* (*Clydonopoma*) Pilsbry, 1933: 127.

*Parachondria* (*Eccritopoma*) Pilsbry, 1933: 128 [type species *Parachondria peasei* Pilsbry, 1933, by original designation].

**Description:** Shells medium to very large for family (to ca. 33 mm length), turbinoid to elongate conic, often decollate. Protoconch of 1.5 smooth or microscopically granulate, minute whorls. Final whorl barely detached from previous whorl for short length. Axial sculpture of wide, flattened, close-set ribs. *Clydonopoma nobilis*, the type species, and *C. poloensis* lack spiral sculpture outside of umbilicus. Remaining species show varying degrees of very weak spiral sculpture, usually limited to subsutural bands and often present only as beads or scalloped edges to axial ribs. Overall sculpture appears very smooth, often shiny, undulating below suture. Suture minutely serrate but lacks fused tufts. Lip double, inner lip usually erect

and separate from outer lip. Adult shell with reflected lip. Lip usually not widely expanded, narrowest facing umbilicus; adnate or very narrowly separated from previous whorl. Color pattern of spiral bands and chevrons, continuous or interrupted, nearly unicolored in some species. Operculum with pseudolamella. Inner marginal tooth of radula broadly rounded with obsolete serrations and very weak denticle on outer side. Animal as in *Chondropomium*.

**Remarks:** Although synonymized with *Chondropomium* by Watters (2006), *Clydonopoma* is here shown to be a distinct genus based on phylogenetic and opercular evidence. Bartsch (1946) placed four species into his *Kisslingia*: *K. hinchensis*, *K. poloense*, *K. bahorucensis* (all Bartsch, 1946), and *K. clenchi* (Pilsbry, 1933) [= *bermudezi* Jaume, 1984]. The latter three are endemic to the Barahona Peninsula. *Kisslingia hinchensis*, the type species of *Kisslingia*, occurs in northern Haiti. Examination shows that the three Barahona taxa are not congeneric with *K. hinchensis* and are better placed in *Clydonopoma*. *Articulipoma* Bartsch, 1946, is very similar to *Clydonopoma* but lacks a pseudolamella.

*Clydonopoma* is endemic to the Sierra de Baoruco and eastern-most Massif de la Selle. Species occur in different habitats than do those of *Chondropomella* and *Chondropomium*. *Clydonopoma* lives in mesic upland forests and pine savannahs whereas *Chondropomium* and *Chondropomella* live on the highly xeric foothills and valleys below among cacti and agave.

The radula differs from that of *Chondropomium* in having the inner marginal very weakly serrate rather than deeply incised. The radula is very similar to *Chondropomella*.

The extent to which the pseudolamella covers the basal portion and radiating ribs of the operculum varies greatly even among individuals of the same population. The pseudolamellate layer may be completely worn away in some specimens revealing the pin-wheel radiating, erect calcareous ribs, rendering the operculum "rhytidopomine" according to the terminology of Henderson and Bartsch (1920). It is probable that the pseudolamellate condition is an extension of that opercular type.

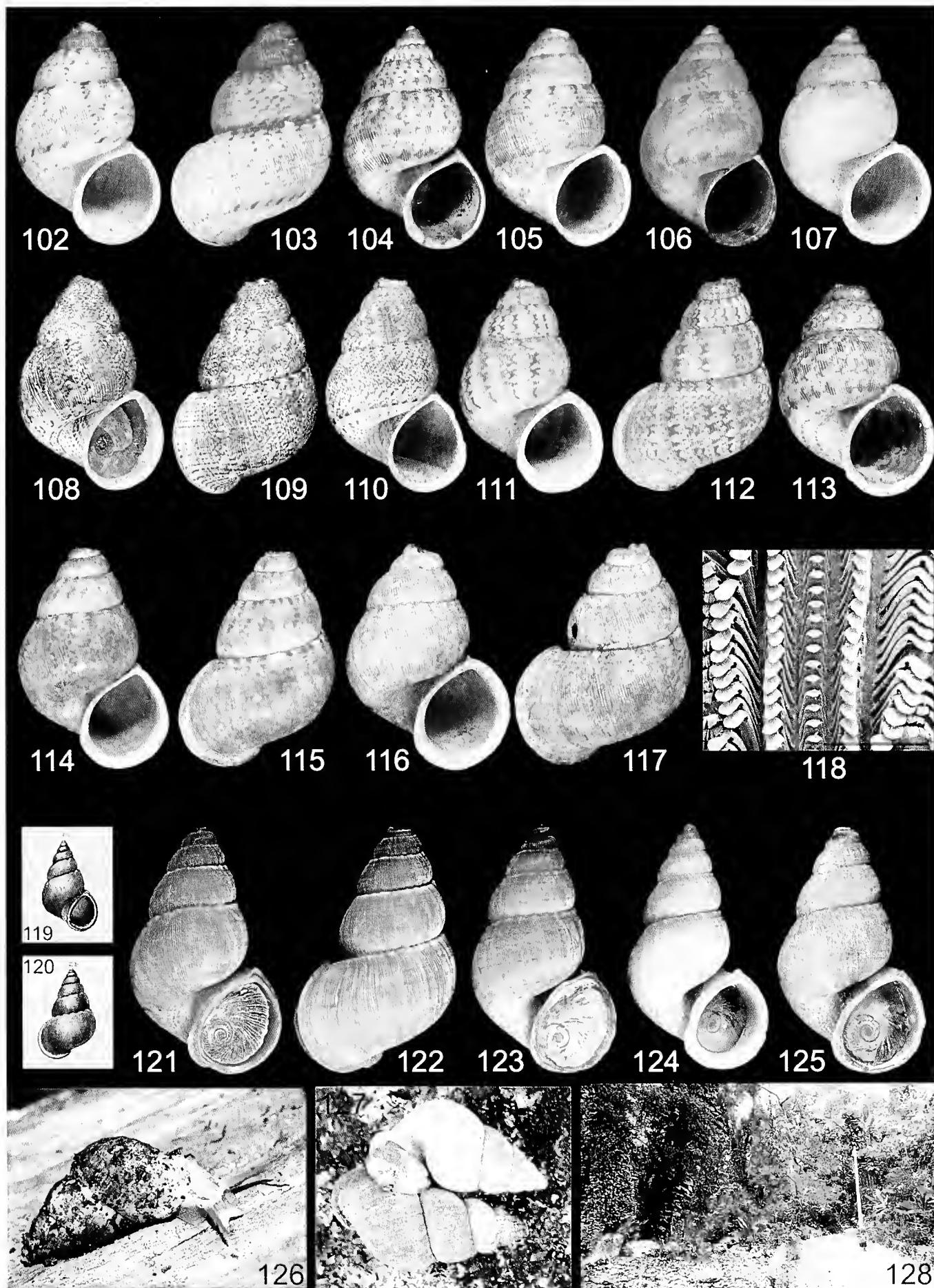
### *Clydonopoma bahorucense* (Bartsch, 1946) (Figures 102–107, 183)

CHRESONYMY

*Kisslingia bahorucensis* Bartsch, 1946: 112, 113–114, pl. 17, fig. 2.

*Licina bahorucensis* (Bartsch, 1946): Watters, 2013: map 1.

**Description:** Shell medium for family (largest adult specimen 15.4 mm maximum length, decollate, including peristome; smallest adult specimen 13.4 mm length, decollate, including peristome), thin, low-spined, umbilicus open but narrow. Protoconch retained in many adult specimens; of 1.5–2 microscopically granulate whorls.



**Figures 102–128.** *Clydonopoma* species. **102–107.** *Clydonopoma bahoricense* (Bartsch, 1946). **102, 103.** USNM 504038, holotype, 14.7 mm. **104.** UF 217965, 15.4 mm. **105.** UF 217965, 13.4 mm. **106.** UF 217965, 14.5 mm. **107.** UF 217965, 14.0 mm. **108–113.** *Clydonopoma bartschi* (Watters, 2012). **108, 109.** UF 446073, holotype, 20.1 mm. **110.** OSUM 36520, paratype, 20.6 mm. **111, 112.** UF 216467, 18.7 mm. **113.** UF 216463, 16.7 mm. **114–117.** *Clydonopoma bermudezi* (Janinc, 1984). **114, 115.** ANSP 160995a, holotype of *Chondropoma clenchi* Pilsbry, 1933, 18.0 mm [photo courtesy of ANSP]. **116, 117.** USNM 426036, paratype, 14.3 mm. **118–128.** *Clydonopoma nobile* (Pfeiffer, 1852). **118.** OSUM 42366, radula. Scale bar = 400  $\mu$ m. **119, 120.** Pfeiffer, 1854a: pl. 13, figs. 2a,b. **121, 122.** G1W 7089a, 28.9 mm. **123.** OSUM 42366, 28.2 mm. **124.** OSUM 42366, 32.4 mm. **125.** G1W 7089b, 26.9 mm. **126.** Living individual. **127.** Individuals mating. **128.** Type locality.

Teleoconch of 3.5–4 whorls, final whorl narrowly adnate with previous whorl. Suture indented, channeled. Peristome single, oval. Outer lip narrow, barely expanded, narrowest facing umbilicus, weakly adnate or just touching previous whorl, minutely or not auriculate posteriorly. Axial sculpture of ca. 150 narrow, erect, widely spaced lamellae. Spiral sculpture of variable number of weak cords extending from suture to mid-whorl in some specimens or covering entire shell in others, weak threads in umbilicus. Intersections of axial and spiral sculpture form weakly scalloped surface. Axial elements render suture finely serrate. Base color white with overlain weak pattern of brown zig-zags and spots, most prominent below suture and on base where they form interrupted bands; overall appearance is pale with limited markings. Markings may appear on lip as well. Operculum with pseudolamella. Anatomy and radula unknown.

**Type Material:** Holotype: USNM 504038 (2 specimens in lot, holotype listed as 14.7 mm long specimen).

**Type Locality:** “Polo District, Bahoruco Mountains, Dominican Republic, at an elevation of 2,000 feet.”

**Type Figured:** Bartsch, 1946, pl. 17, fig. 2.

**Distribution:** Bartsch (1946) listed specimens from the Polo region, Loma de Cielo (Capo de Cielo), and 1.6 km north of Maniel Viejo. We add the area of Angostura in Independencia Province. With the exception of the Angostura specimen at 42 m elevation, all localities are between 600–1070 m in the eastern and northeastern Sierra de Baoruco.

**Habitat:** Mesic limestone ravines; all of the UF sites (below) have been cleared for coffee groves. The Angostura site has been quarried.

**Other Material Examined (46 Specimens): Dominican Republic. Barahona Province.** UF 217966(19), 910 m, 5 km NNE of Polo; UF 217974(5), 910 m, 7 km NNE of Polo; UF 217968(3), 710 m, 7 km NNE of Polo; UF 217965(18), 910 m, 14 km S of Cabral. **Independencia Province.** OSUM 42371(1), 42 m, quarried area along road to Angostura, 1 km NNW of Angostura, 18.3412° N, –71.4207° W.

**Variation Among Specimens:** This species and *C. titatum* show more variation in color than any other *Clydonopoma*, ranging from heavily patterned with brown chevrons and blotches to nearly all white. The subsutural row of evenly spaced brown markings seems to be consistent.

**Comparison with Other Species:** This species has the most developed sculpture of the species of *Clydonopoma*. The intersections of the spiral and axial sculpture form an extensive scalloped surface that is not seen in other species. *Clydonopoma bermudezi* is most similar to this species but only has a few weak scalloped spiral cords below the suture; it is less elongate and smaller as well. *Clydonopoma bahoruicense* is sympatric with *C. poloense*

but is smaller and has a more channeled suture; *C. poloense* lacks spiral sculpture outside of the umbilicus.

**Etymology:** Bahoruco Mountains, Dominican Republic.

### *Clydonopoma bartschi* (Watters, 2012)

(Figures 108–113, 183)

CHRESONYMY

*Licina bartschi* Watters, 2012: 13, figs. 45–47; Watters, 2013: map 1, plate 1, fig. 5.

**Description:** Shell medium for family (largest adult specimen 19.9 mm maximum length, decollate, including peristome; smallest adult specimen 10.3 mm maximum length, including peristome), solid, conic, umbilicus minute. Protoconch whorls decollate in adults, consisting of 1.5 smooth, prominent whorls, well-delimited from teleoconch. Teleoconch of 4 whorls, final whorl detached just before peristome. Suture deeply channeled. Peristome single, thick, tear drop-shaped. Lip narrow, barely expanded on outer side, auricle absent. Spiral sculpture present only as 3–5 very feeble cords below suture rendering axial sculpture scalloped, 7–9 cords in umbilicus. Axial sculpture of narrow, fine ribs separated by 2–3x their width, ca. 150 on final whorl, forming minute cusps at suture. Suture serrate. Background color glossy pale tan with complex pattern of dense, brown, very fine, zigzag markings axially aligned, sometimes forming interrupted spiral bands on base and within umbilicus; growth rests marked by axial rows of tiny dark spots; suture with pattern of alternating white and dark brown patches; markings persist on both sides of peristome and are visible through inside of shell. Operculum paucispiral with pseudolamella that extends 3/5ths of way to outer margin, corneous portion with fine granular deposit. Anatomy and radula unknown.

**Type Material:** Holotype: UF 446073; Paratype 1: NHMUK 20110338, slightly juvenile; Paratype 2: OSUM 36520; both paratypes from the type locality.

**Type Locality:** “9.5 km ENE of Las Mercedes, Pedernales Province, Dominican Republic, on a mountain top at 1,300 m elevation.”

**Type Figured:** Watters 2012, figs. 45, 46.

**Distribution:** This is an upland species usually found above 1000 m in the western Sierra de Baoruco.

**Habitat:** On limestone hills and in ravines under rocks in scrub and pine savannah.

**Other Material Examined (83 Specimens): Dominican Republic. Pedernales Province.** GTW 14630d(1), 1285 m, abandoned quarry near end of road that runs from Cabo Rojo N past Las Mercedes into Sierra de Baoruco, 18.1203° N, –71.5725° W; UF 216467(7), 1000 m, W rim of Hoya de Pelempito; UF 216463(29), 1410 m,

Loma El Aceitillar; UF 249186 (10), 240 m, 19 km N of Pedernales; UF 217958(46), 1510 m, 20 km N of Las Mercedes.

**Variation Among Specimens:** Specimens are very uniform in most characteristics but differ in the degree of coloration. The base color varies from pale tan to a greyish east.

**Comparison with Other Species:** *Clydonopoma bartschi* is very similar to *C. peasei* and *C. poloense*. All are large, similarly colored species. *Clydonopoma poloense* lacks the spiral grooves below the suture seen in *C. bartschi* and *C. peasei*. *Clydonopoma peasei* is more obviously turbinoid than the other two taxa. *Clydonopoma nobile* is the largest of the genus and is usually almost unicolored, often with a purplish tinge. *Clydonopoma pumilum* is smaller, has a well-developed outer lip and a pattern of minute dots and dashes rather than the complex pattern of chevrons and bands seen in *C. bartschi*, *C. poloense*, and *C. peasei*. *Clydonopoma pumilum* differs from *C. bahoruensis* and *C. bermudezi* in the lack of spiral sculpture on the posterior half of the whorl. Nevertheless, all of these species are closely related and similar in appearance.

**Remarks:** This species was originally placed in *Licina*, a genus requiring a thorough review. *Licina* has a pseudolamellate operculum like *Clydonopoma* but possesses distinct spiral sculpture over the entire shell. Species assigned to *Licina* probably represent several genera. The original images of this species in 2012 were unfortunately vertically foreshortened by the printer. No material was available for phylogenetic study.

**Etymology:** Paul Bartsch (1871–1960), malacologist at the US National Museum and expert on the Annulariidae.

### *Clydonopoma bermudezi* (Jaume, 1984)

(Figures 114–117, 184)

CHRESOONYMY

*Chondropoma* (*Chondropomium*) *clenchi* Pilsbry, 1933: 126, pl. 9, figs. 2, 3 [*non Chondropoma ernesti clenchi* Aguayo, 1932b].

*Kisslingia clenchi* (Pilsbry, 1933); Bartsch, 1946: 112, 115, pl. 17, fig. 1.

*Licina*? *clenchi* (Pilsbry, 1933); Baker, 1964: 169.

*Kisslingia bermudezi* Jaume, 1984: 3 [replacement name, see Remarks].

*Chondropoma* (*Chondropomium*) *compressa* Boyko and Cordeiro, 2001: 30 [replacement name, see Remarks].

*Licina clenchi* (Pilsbry, 1933); Watters, 2013: map 1.

**Description:** Shell medium for family (largest adult specimen 18.0 mm maximum length, decollate, including peristome, smallest adult specimen 13.0 mm maximum length, including peristome), solid, conic, umbilicus minute. Protoconch whorls usually retained

in adults, consisting of 1.5 smooth whorls, well-delimited from teleoconch. Teleoconch of 3.5–4 whorls, final whorl detached just before peristome. Suture deeply channeled. Peristome single, thick, tear drop-shaped. Outer lip narrow, barely expanded on outer side, auricle weak or absent. Spiral sculpture present as ca. 8 wide, undulating cords below suture, gradually diminishing in strength, and as ca. 10 cords in umbilicus. Axial sculpture of numerous narrow, fine closely-set ribs, ca. 110 on final whorl, forming minute, elongate cusps at suture. Suture serrate. Intersections of spiral and axial sculpture finely beaded or scalloped. Background color white or pale tan with complex pattern of faint, brown, very fine, zigzag markings axially aligned, sometimes forming interrupted spiral bands on base; suture with pattern of alternating white and dark brown patches; markings do not persist onto either side of lip. Rarely almost entirely patternless, but sutural markings are consistent. Operculum paucispiral with pseudolamella that extends 3/5ths of way to outer margin, corneous portion with fine granular deposit. Anatomy and radula unknown.

**Type Material:** Holotype: ANSP 160995a; Paratypes: 81534(4); USNM 426036(2); AMNH 81534(3).

**Type Locality:** “Sr. Del Monte coffee plantation, Station 85, between the main baté and the top of Alies in the coffee finca proper, and in a verdant gully near Salvation, at about 3,000 feet.” As Pilsbry (1933: 121) pointed out, Salvation was the name of a division of the Del Monte coffee finca and “of course not to be found on any published map.”

**Type Figured:** Pilsbry, 1933, pl. 9, figs. 2, 3.

**Distribution:** Known only from the type locality in the eastern Sierra de Baoruco.

**Habitat:** Pilsbry (1933: 122) described the habitat at the type locality: “a gully near Salvation; the walls are steep and with luxuriant growth of trees and underbrush; the sides of the nearly waterless stream bed very wet, mossy, with deep humus, and lined with boulders.”

**Other Material Examined (2 Specimens): Dominican Republic.** USNM 426036(2), from type locality.

**Variation Among Specimens:** Only two specimens have been examined by us.

**Comparison with Other Species:** See under *C. bartschi*.

**Remarks:** This species was renamed twice based on the fact that *Chondropoma clenchi* Pilsbry, 1933, was a junior primary homonym of *Chondropoma ernesti clenchi* Aguayo, 1932. Jaume (1984) created the replacement name *Kisslingia bermudezi*. Unaware of this action, Boyko and Cordeiro (2001) also created a replacement name, *Chondropoma* (*Chondropomium*) *compressa*. The name

of this taxon thus becomes *Chydonopoma bermudezi* Jaume, 1984. No material was available for phylogenetic study.

**Etymology:** *Chondropoma clenchi* Pilsbry, 1933: William James Clench (1897–1984), American malacologist, Museum of Comparative Zoology, Harvard University. *Kisslingia bermudezi* Jaume, 1984: Pedro Joaquín Bermúdez y Hernández (1905–1979), Cuban naturalist and geologist. *Chondropoma compressa* Boyko and Cordeiro, 2001: *L. compressa*, “to clench,” apparently an unfortunate pun on Clench.

***Clydonopoma nobile* (Pfeiffer, 1852)**

(Figures 118–128, 183)

CHRESOONYMY

*Tudora nobilis* Pfeiffer, 1852a: 252; Pfeiffer, 1853a: 176; Pfeiffer, 1858b: 128; Bland, 1861: 355; Pfeiffer, 1865: 138; Pfeiffer, 1876: 185; Kobelt, 1880: 277; Crosse, 1891: 177.

*Cyclostoma* (*Tudora*) *nobile* (Pfeiffer, 1852): Pfeiffer, 1854a: 142, pl. 13, figs. 2a–c.

*Cyclostoma nobile* (Pfeiffer, 1852): Pfeiffer, 1854c: pl. 47, figs. 27–28; Pfeiffer, 1854d: 366–367.

*Cistula* (*Tudora*) *nobilis* (Pfeiffer, 1852): Adams and Adams, 1856: 294.

*Chondropoma* (*Chondropomium*) *nobilis* (Pfeiffer, 1852): Henderson and Bartsch, 1920: 60.

*Parachondria* (*Chydonopoma*) *nobilis* (Pfeiffer, 1852): Pilsbry, 1933: 127–129, pl. 6, figs. 14, 16–19; Wenz, 1939: 546, fig. 1454.

*Chydonopoma* (*Chydonopoma*) *nobile* (Pfeiffer, 1852): Bartsch, 1946: 135–136, pl. 21, fig. 3.

*Chondropomium nobile* (Pfeiffer, 1852): Watters, 2006: 63, 375; Watters, 2012: 13–14, fig. 48, 53 [animal], 58 [habitat]; Watters, 2013: 4, pl. 2, fig. 14, map 1.

*Chydonopoma nobile* (Pfeiffer, 1852): Watters, 2013: map 1.

**Description:** Shell very large for family (largest adult specimen 32.3 mm maximum length, decollate, including peristome, smallest adult specimen 25.1 mm maximum length, including peristome), very solid, high-spined, umbilicus open but minute. Protoconch whorls often retained in adults, consisting of 1.5 smooth, blunt white whorls, well-delimited from teleoconch. Teleoconch of 4–5 whorls, final whorl detached ca. ¼ length before peristome. Suture deeply channeled. Peristome double, thick, tear drop-shaped. Inner lip thickened, prominent, erect, projecting well beyond outer lip. Outer lip thick, narrowly expanded, lamellate, undulating anteriorly, often fused with inner lip on umbilical side, with minute posterior auricle. Outer lip with concave or sinuous undulation on outer margin. Spiral sculpture present as ca. 12–20 wide, thick cords in umbilicus. Axial sculpture of ca. 190 very narrow erect lamellae, widely spaced on center of whorl, gathered together on base; lamellae grouped in growth series, sometimes anastomosing where shell has

been damaged. Suture undulating and serrate, each axial element slightly enlarged and minutely blade-like. Background color white, brown, or purplish with 10–15 spiral bands of very minute spots alternating with very narrow interrupted spiral markings; markings do not persist onto either side of lip. Operculum paucispiral with pseudolamella that extends 3/5ths of way to outer margin, but pseudolamella may be completely worn away exposing underlying pin-wheel erect ribs. Animal white with pale grey foot and pale grey base of snout; large diffuse grey patch between eyes; tentacles orange. Radula as in genus.

**Type Material:** Three specimens glued to board at NHMUK, unnumbered, none marked with an “X,” label reads “Haiti;” these are possible syntypes but do not match Pfeiffer, 1854a: pl. 13, figs. 2a–c.

**Type Locality:** “in insula Haiti.” Restricted here to Virgen de San Rafael, Barahona Province, Dominican Republic.

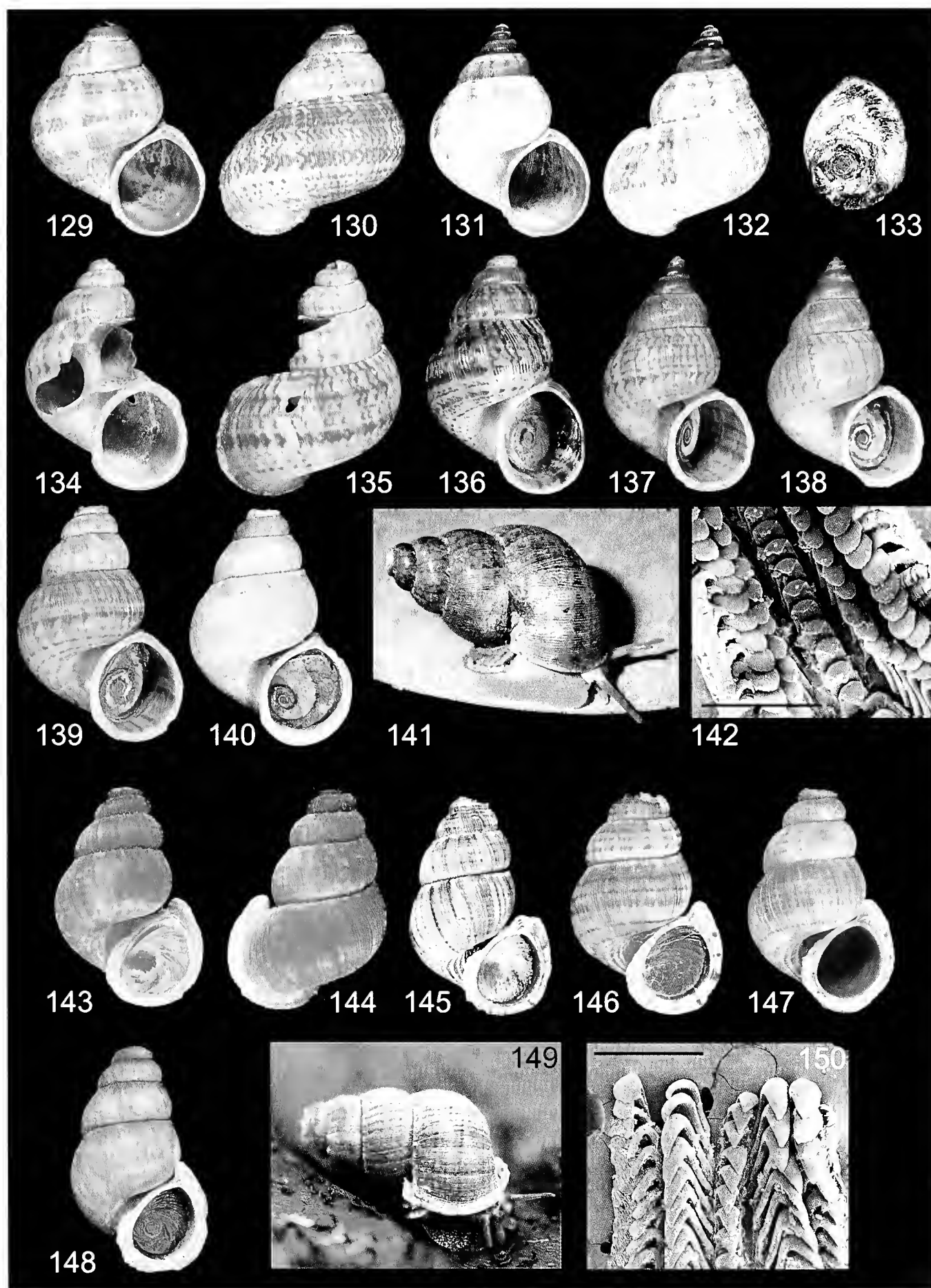
**Type Figured:** Pfeiffer, 1854a, pl. 13, figs. 2a–c.

**Distribution:** This species occupies a restricted coastal range along the eastern Barahona Peninsula from Paraíso north and then curves inland along the northeastern Sierra de Baoruco to Barahona and Cabral. Locally common.

**Habitat:** Under limestone rocks and in stone fence crevices in verdant, mesic forest, found to ca. 450 m elevation. Individuals were observed actively crawling about and mating in the early morning but they had disappeared by late morning. It occurs with uropygid arachnids, which may be predaceous on this snail; shells often show signs of repaired breakage. This species can occupy lower elevations than its congeners by virtue of its coastal distribution in the prevailing offshore winds that create a mesic habitat at sealevel.

**Other Material Examined (178 Specimens): Dominican Republic. Barahona Province.** UF 217802 (10), UF 217810(2), 6 km SSW of Cabral; UF 217809(2), 20 m, 4 km E of Cachon; UF 217803(16), UF 217805(13), 200 m, 5 km SE of Barahona; UF 217811(6), UF 217812 (4), 300 m, 5 km SE of Barahona; UF 217815(25), 450 m, 5 km SE of Barahona; UF 155894(11), 15 km S of Barahona; GTW 7089a(1), 16 km S of Barahona; UF 217813(4), 400 m, 2 km SW of La Guázara; UF 217808 (2), 180 m, 4 km NE of La Guázara; UF 217807(2), 150 m, 6 km NE of La Guázara; GTW 7089e(2), 18 m, cleared area off RD 44, near Juan Esteban, 18.1294° N, –71.0697° W; UF 45691(25), 10 km NNE of Paraíso; GTW 7089b(10), GTW 7089c(1), OSUM 42366(10), Villa Miriam, Virgen de San Rafael, ca. 7 km NNE of Paraíso, 18.4601° N, –69.6096° W; UF 217814(25), 30 m, 4 km SW of La Cienaga; UF 217804(10), UF 217806(10), 30 m, 6 km SW of La Cienaga.

**Variation Among Specimens:** The base color of the shell varies from white to a purplish-brown color but the very fine spiral bands and dots are always present.



**Figures 129–150.** *Clydonopoma* species. **129–133.** *Clydonopoma peasei* (Pilsbry, 1933). **129, 130.** ANSP 160976, holotype, 22.0 mm [photo courtesy of ANSP]. **131, 132.** USNM 426043, paratype, 21.4 mm. **133.** USNM 426043, paratype, operculum, 7 mm length. **134–142.** *Clydonopoma poloense* (Bartsch, 1946). **134, 135.** USNM 504040, holotype, 20.5 mm. **136.** OSUM 42372, 20.4 mm. **137.** UF 217969, 23.7 mm. **138.** UF 217969, 21.5 mm. **139.** UF 217969, 20.8 mm. **140.** UF 217970, 23.0 mm. **141.** Living individual, note supernumerary eye on left tentacle. **142.** OSUM 42372, radula. Scale bar = 300  $\mu$ m. **143–150.** *Clydonopoma pumilum* (Watters and Duffy, 2010). **143, 144.** UF 420734, holotype, 15.0 mm. **145.** GTW 7172b, 19.9 mm. **146.** GTW 7172c, 15.0 mm. **147.** GTW 7172b, 17.3 mm. **148.** UF 217798, 20.0 mm. **149.** Living individual. **150.** GTW 7172b, radula. Scale bar = 200  $\mu$ m.

**Comparison with Other Species:** See under *Chydonopoma bartschi*. The large size, lamellate sculpture, thick double lip, and peculiar coloration are unique in this group. The lip of *C. titanum* is even more expanded and broadly attached to the previous whorl.

**Remarks:** The outer lip is sinuate recalling the male shell of some other annulariids such as *Tudora*. But it appears that all individuals, male and female, have this characteristic.

**Original Description:** Pfeiffer, 1852a: 252. From the Latin. "Shell umbilicate, ovate-turret, solid, crowded longitudinal course plications, a little shining, brownish-violet; spire elongated, conic, entire, obtuse; suture with crowded white crenulations; remaining 7 whorls moderately convex, last narrowly solute before, base concentrically striate; aperture vertical, irregularly oval, inside brown; lip white, double: inner narrowly erect, a little expanded, upper margin attached angle, columella very shortly arched, outer narrowly expanded everywhere. Operculum paucispiral, deep oblique sulcus."

**Etymology:** *L. nobilis*, noble.

### ***Chydonopoma peasei* (Pilsbry, 1933)**

(Figures 1, 129–133, 182)

#### CHRESONYMY

*Parachondria* (*Eccritopoma*) *peasei* Pilsbry, 1933: 128–129, pl. 6, figs. 5–7; Wenz, 1939: 545, fig. 1453; Richards and Old, 1969: 69; Watters, 2006: 396.

*Chydonopoma* (*Eccritopoma*) *peasei* (Pilsbry, 1933): Bartsch, 1946: 136–137, pl. 21, fig. 2.

*Licina peasei* (Pilsbry, 1933): Baker, 1964: 170.

*Chondropomum peasei* (Pilsbry, 1933): Watters, 2006: 63, 396.

*Chydonopoma peasei* (Pilsbry, 1933): Watters, 2013: 4, map 1.

**Description:** Shell large for family (largest adult specimen 22.0 mm maximum length, decollate, including peristome, smallest adult specimen 21.4 mm maximum length, including peristome), thin, turbinoid, umbilicus wide and open. Protoconch whorls may be retained in adults, consisting of 2 dark, microscopically granulate whorls, well-delimited from teleoconch. Teleoconch of 3.5 whorls, final whorl detached just before peristome. Suture deeply channeled. Peristome double, oval. Inner lip erect, projecting slightly beyond the outer lip. Outer lip narrow, barely expanded on outer side, lamellate, with weak posterior auricle. Spiral sculpture present as ca. 6 wide, undulating cords below suture, gradually diminishing in strength, and as ca. 13 cords within umbilicus. Axial sculpture of numerous narrow, fine, closely-set ribs, ca. 230 on final whorl, forming minute, elongate cusps at suture. Suture serrate. Intersections of spiral and axial sculpture finely beaded or scalloped. Background color white or pale tan with complex pattern of faint, brown, zigzag markings spirally aligned; markings do not persist onto either side of lips. Early whorls

darker. Inside margin of aperture yellow. Operculum paucispiral with pseudolamella that extends ½ of way to outer margin, remainder with pin-wheel arranged, erect, calcified ribs. Anatomy and radula unknown.

**Type Material:** Holotype: ANSP 160976a (as L in Richardson et al., 1991); Paratypes: ANSP 374376 (as PL in Richardson et al., 1991); USNM 426043; P: Pease coll.

**Type Locality:** "Sr. Del Monte's plantation, 5 or 6 miles west of Barahona, at Station 85, in a verdant gully near Salvation, at about 3,000 ft." See "Type locality" under *C. cleuchi*, above.

**Type Figured:** Pilsbry, 1933, pl. 6, figs. 5–7.

**Distribution:** *Chydonopoma peasei* is known only from the type locality west of Barahona in the Sierra Baoruco.

**Habitat:** The holotype was collected in the same location as *C. bernudezi*, see above.

**Variation Among Specimens:** Only type specimens seen.

**Comparison with Other Species:** See under *Chydonopoma bartschi*. If consistent, the yellow color inside the aperture is unique. It is very similar to *C. poloense* found just to the south in the same mountain range. It is less elongate and has stronger spiral cords in the umbilicus than does *C. poloense*.

**Remarks:** This species is known only from the type lots. This is the type species of *Eccritopoma* Pilsbry, 1933, which was differentiated primarily by the presence of a few weak spiral grooves below the suture. We consider this a species-level feature; *Eccritopoma* was synonymized under *Chydonopoma* by Watters (2006). No material was available for phylogenetic study.

**Etymology:** Daniel C. Pease, American Museum of Natural History, collector of the types. Pease collected in Hispaniola in 1932.

### ***Chydonopoma poloense* (Bartsch, 1946)**

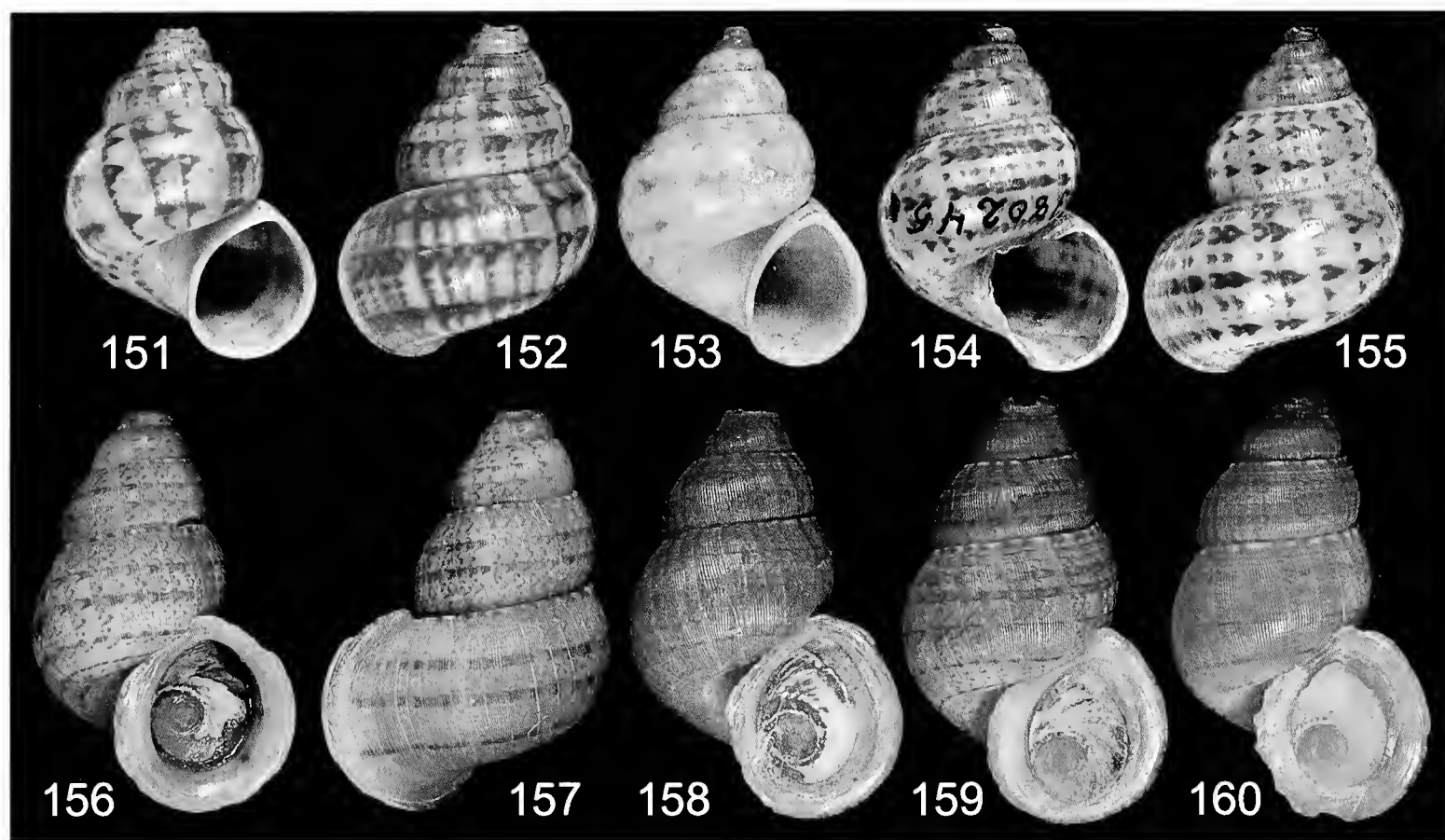
(Figures 2, 134–142, 182)

#### CHRESONYMY

*Kisslingia poloensis* Bartsch, 1946: 112, 114–115, pl. 17, fig. 4; Watters, 2006: 415.

*Licina poloensis* (Bartsch, 1946): Watters, 2006: 75, 415; Watters, 2012: 13; Watters, 2013: map 1.

**Description:** Shell large for family (largest adult specimen 23.7 mm maximum length, decollate, including peristome, smallest adult specimen 18.9 mm maximum width, including peristome), solid, conic, umbilicus wide. Protoconch whorls often retained in adults, consisting of 1.5 smooth tan whorls with dark median spiral band, well-delimited from teleoconch. Teleoconch of 4 whorls, final whorl detached just before peristome. Suture channeled. Peristome single, thick,



**Figures 151–160.** *Clydonopoma* species. **151–155.** *Clydonopoma?* *subglobosum* (Bartsch, 1946). **151, 152.** USNM 504141, paratype, 18.0 mm. **153.** USNM 380218, 18.3 mm. **154, 155.** USNM 380245, 19.9 mm. **156–160.** *Clydonopoma titanum* new species. **156, 157.** OSUM 42351, holotype, 29.1 mm. **158.** GTW 16816a, 27.1 mm. **159.** UF 492090, paratype 3, 28.1 mm. **160.** BMSM 121709, paratype 4, 27.9 mm.

tear drop-shaped. Outer lip narrow, barely expanded on outer side, auricle weak or absent. Spiral sculpture absent except for 4–6 cords in umbilicus. Axial sculpture of numerous narrow, fine, closely-set rounded ribs, ca. 140 on final whorl, often arranged in growth series, forming minute, blade-like cusps at suture. Suture serrate. Background color white or pale tan with complex pattern of brown zigzag or chevron markings axially aligned, sometimes forming interrupted spiral bands on base; markings do not persist onto either side of lip; umbilicus without markings. Rarely almost entirely patternless. Early teleoconch whorls may be colored darker brown or purplish. Operculum with thick pseudolamella divided into two regions: outer half of spiral with very coarse erect lamellae, inner half similar but at lower level. Radula as in genus. Animal white with pale grey foot and head patch between eyes, tentacles pale orange.

**Type Material:** Holotype: USNM 504040.

**Type Locality:** “Near Polo, Bahoruco Mountains, Dominican Republic.”

**Type Figured:** Bartsch, 1946, pl. 17, fig. 4.

**Distribution:** This species is known from the Sierra Baoruco in the vicinity of Polo and La Cueva.

**Habitat:** This is an upland species known only above 700 m elevation. It lives under fossil limestone blocks in mesic, well-vegetated or forested areas and ravines. Portions of its range are now in coffee and banana groves.

**Other Material Examined (60 Specimens): Dominican Republic. Barahona Province.** GTW 16226a(2), 996 m, quarried area along Carr Los Lirios el Charco (dirt road), 18.0965° N, –71.2516° W; OSUM 42372(9), 1120 m, along Carr Los Lirios el Charco (dirt road) near village of Carbon de Polla, 18.1175° N, –71.2622° W; UF 217973(1), 910 m, 14 km S of Cabral; UF 217976(3), 1 km N of Los Auyamas; UF 217972(1), 4 km NE of Los Auyamas; UF 217975(2), 765 m, 2 km NNE of Polo; UF 217970(9), 990 m, 5 km NNE of Polo; UF 45604(2), 1020 m, 6 km SSE of Polo; UF 217971(4), 910 m, 7 km NNE of Polo; UF 217969(22), 1040 m, 5 km SE of Polo; UF 217967(3), 940 m, 9 km SE of Polo; UF 45616(2), 980 m, 7 km SSE of Polo.

**Variation Among Specimens:** Specimens vary in the strength of the background color (white to tan) and the pattern (dark chevrons to absent).

**Comparison with Other Species:** See under *Clydonopoma bartschi*.

**Remarks:** The holotype is a broken shell collected by William L. Abbott between 1916–1923. The species was not collected again until the 1970s.

**Etymology:** Polo, Dominican Republic.

***Clydonopoma pumilum* (Watters and Duffy, 2010)**  
(Figures 143–150, 182)

CHRESOONYMY

*Chondropomium pumilum* Watters and Duffy, 2010: 8–10, figs. 27–30; Watters, 2012: 14, figs. 49, 54 [animal]; Watters, 2013: 4, pl. 2, fig. 15, map 1.

**Description:** Shell medium for family (largest adult specimen 20.0 mm length, decollate, including peristome; smallest adult specimen 14.2 mm maximum length, decollate, including peristome), solid, conic, umbilicus wide. Protoconch whorls unknown, decollate in adults. Teleoconch of 4.25–4.5 whorls, final whorl adnate except for immediately behind peristome. Suture channeled. Peristome double, thick, tear drop-shaped. Outer lip widely expanded but narrowest facing umbilicus, scalloped on anterior margin, produced into prominent, concave auricle posteriorly. Inner lip very short and erect. Spiral sculpture present only as few feeble cords in umbilicus. Axial sculpture of numerous closely spaced, thin, low lamellae, occasionally anastomosing. Axial lamellae slightly elongated at suture into blade-like cusps. Background color tan or brownish purple with diffuse narrow, spiral bands brown bands. Outer lip white. Operculum paucispiral with pseudolamella. Animal with grey foot, snout, and base of tentacles; head white with dark grey mottling between tentacles; distal portion of tentacles orange. Radula with broad, triangular inner marginal teeth with obsolete, minute denticles; rachidian and lateral teeth unicuspid and very elongate.

**Type Material:** Holotype: UF 420734; Paratypes: OSUM 32484(1); NHMUK 1996350(1).

**Type Locality:** “Dominican Republic, Barahona, Pedernales Province, 19–32 km N of Cabo Rojo, ~500–900 m.”

**Type Figured:** Watters and Duffy, 2010, figs. 28, 29.

**Distribution:** Known only from ca. 400–1500 m elevation on the western face of the Sierra de Baoruco.

**Habitat:** Under limestone rocks in upland coniferous forests; some areas burnt over.

**Other Material Examined (98 Specimens): Dominican Republic, Pedernales Province.** GTW 7172a(1), 760 m, 21–24 km N of Cabo Rojo; GTW 7172b(9), 1300 m, on road to Las Mercedes, 21 km NE of Pedernales; UF 217794(12), 1080 m, 12 km N of Las Mercedes; UF 217793(12), 1510 m, 20 km N of Las Mercedes; GTW 7172c(1), 1285 m, abandoned quarry near end of road that runs from Cabo Rojo N past Las Mercedes into Sierra de

Baoruco, 18.1203° N, –71.5727° W; UF 217798(18), 1410 m, Loma El Aceitillar, 12 km ENE of Las Mercedes; UF 217799(12), UF 217801(8), 1300 m, Loma El Aceitillar, 19 km ENE of Las Mercedes; UF 217797(6), 39 road km N of Cabo Rojo; UF 217800(3), 1000 m, W rim of Hoyo de Pelempito; UF 217795(14), UF 217796(2), 380 m, 3 km N of Nigueron [not found].

**Variation Among Specimens:** Specimens differ primarily in the background color, varying from nearly uniform white to dark purplish brown.

**Comparison with Other Species:** See under *Clydonopoma bartschi*.

**Etymology:** *L. pumilum*, dwarfish, a miniature *C. nobile*.

***Clydonopoma? subglobosum* (Bartsch, 1946)**  
(Figures 151–155).

CHRESOONYMY

*Incertipoma subglobosum* Bartsch, 1946: 171–172, pl. 29, fig. 6; Watters, 2006: 495.

*Chondropomium subglobosum* (Bartsch, 1946): Watters, 2006: 63, 495.

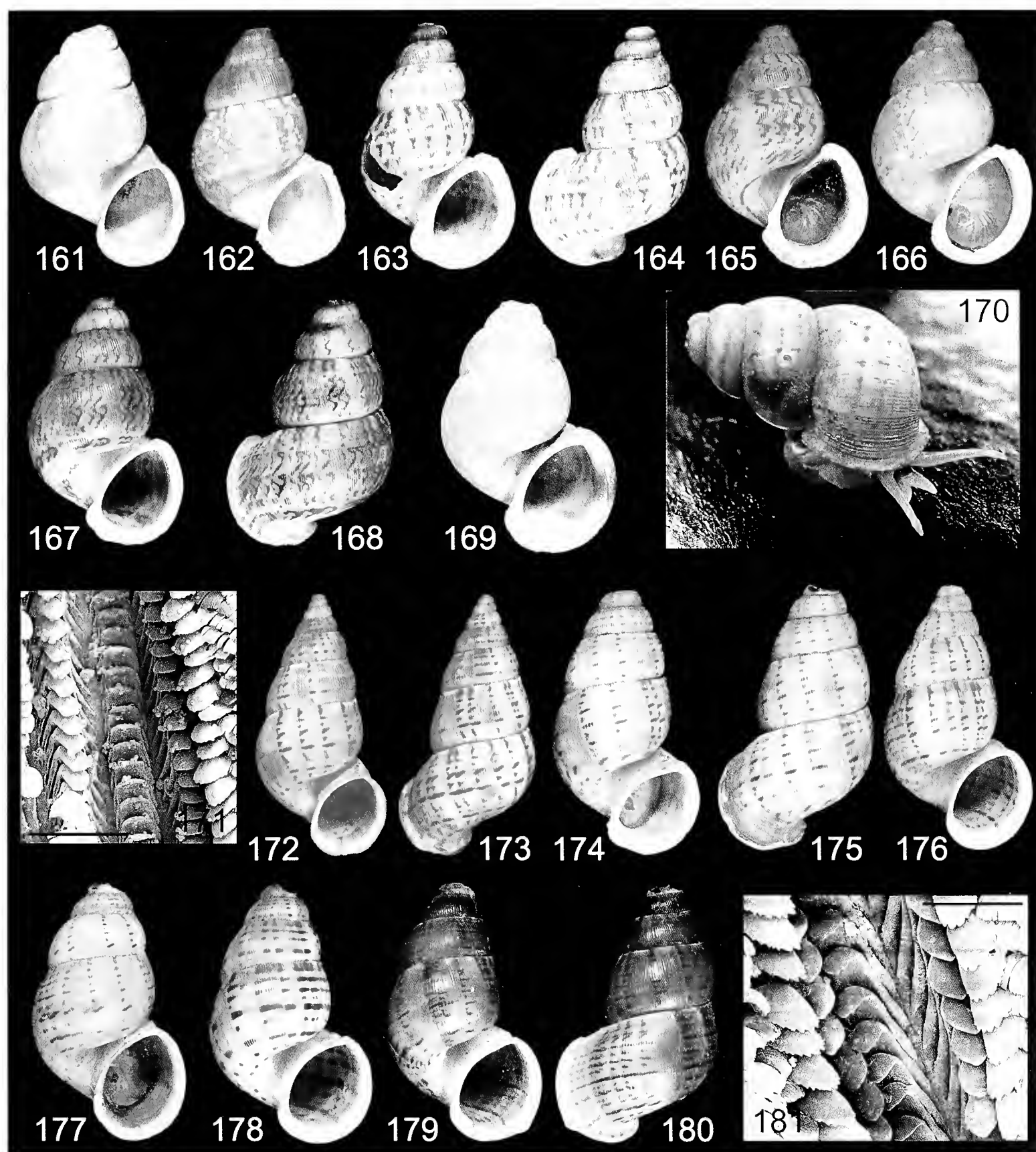
**Description:** Shell large for family (largest adult specimen 22.0 mm length, decollate, including peristome; smallest adult specimen 18.3 mm maximum length, decollate, including peristome), solid, turbinoid, umbilicus wide, polished. Protoconch whorls of 2 brown, smooth whorls, usually decollate in adults. Teleoconch of 4–4.5 whorls, final whorl adnate except for immediately behind peristome. Suture indented but not channeled. Peristome single, tear drop-shaped. Lip scarcely expanded, posterior auricle lacking. Spiral sculpture present only as single thread in umbilicus. Axial sculpture of numerous closely spaced, flat cords on early whorls, obsolete by final whorl. Suture smooth on final whorl. Background color white patterned with brown spiral bands of dots alternating with 3 spiral bands of triangular brown markings. Lip white. Operculum, anatomy, and radula unknown.

**Type Material:** H: USNM 504141.

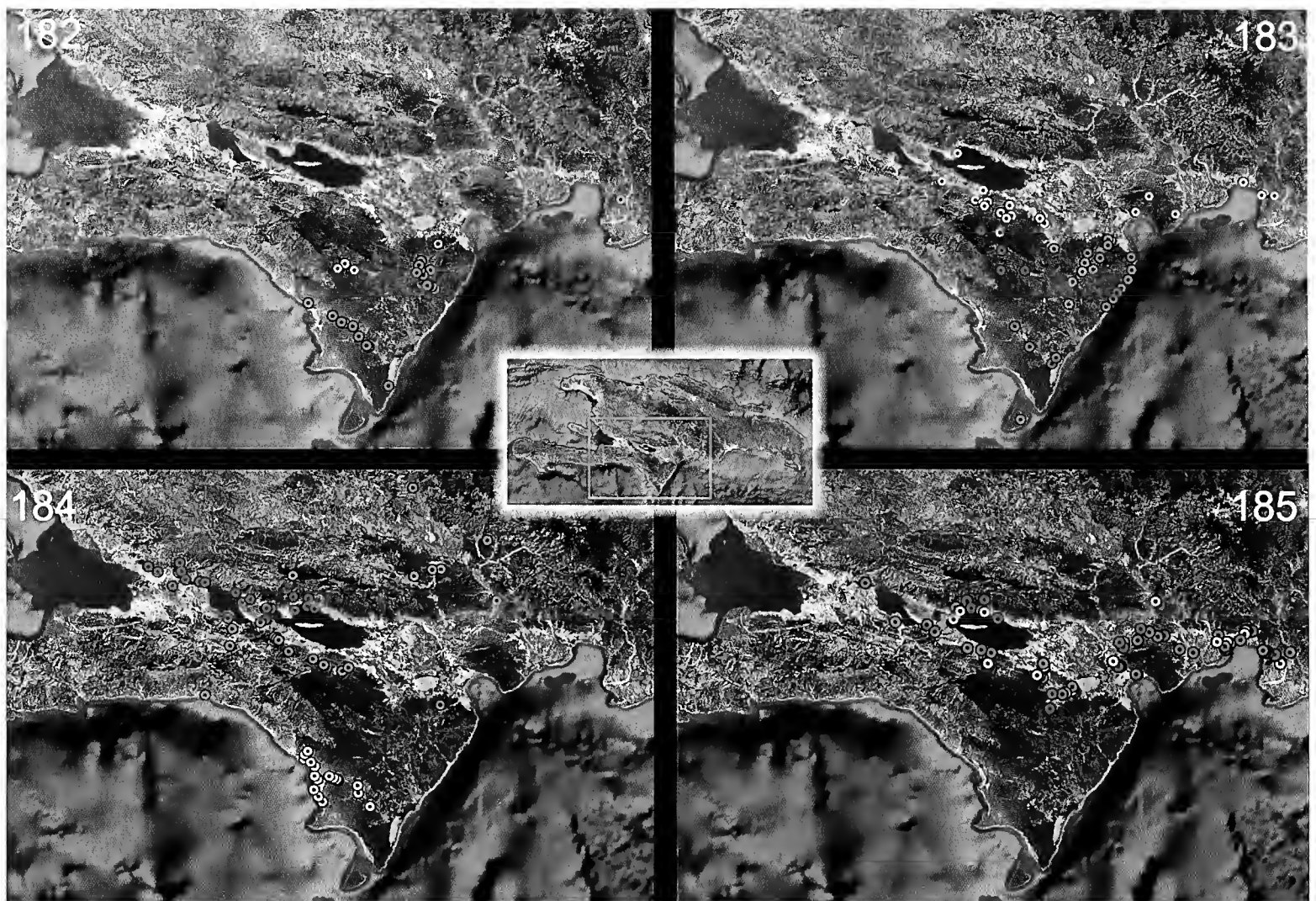
**Type Locality:** “Trou Louise, Gonave Island.” This is the place now known as Platon Trou Louis.

**Type Figured:** Bartsch, 1946, pl. 29, fig. 6.

**Distribution:** Originally recorded from Île de la Gonâve and Petit-Goâve. Bartsch (1946) listed Trou Louise, South Abricots, and Point Fantasque on Île de la Gonâve but only the first locality has been located by us on that island. There is a Point Fantasque at the entrance to Cayemites Bay on the mainland on the north shore of the Tiburon Peninsula across from Île de la Gonâve (Wyman, 1874). It is probable that Bartsch mislocated Point Fantasque on Île de la Gonâve. Petit-Goâve is a town also on the north shore of the peninsula. If our localities are correct then this species lives on Île de la Gonâve and on the



**Figures 161–181.** *Superbipoma* species. **161–171.** *Superbipoma asymmetricum* (Pilsbry, 1933). **161.** ANSP 46656, lectotype, 18.2 mm [photo courtesy of ANSP]. **162.** *Chondropoma curiquillense* Pilsbry, 1933. ANSP 146715, holotype, 23.8 mm [photo courtesy of ANSP]. **163, 164.** USNM 471939, 18.6 mm. **165.** UF 216851, 25.8 mm. **166.** UF 216851, 25.7 mm. **167, 168.** OSUM 42375, 26.9 mm. **169.** USNM 471937, 25.7 mm. **170.** Living individual. **171.** OSUM 42364, radula. Scale bar = 200  $\mu$ m. **172–181.** *Superbipoma superbum* (Henderson and Simpson, 1902). **172, 173.** USNM 168798, holotype, 27.6 mm. **174, 175.** UF 119165, 24.8 mm. **176.** UF 216852, 28.5 mm. **177.** UF 216854, 22.6 mm. **178.** GTW 7086b, 23.8 mm. **179, 180.** GTW 7086b, 25.5 mm. **181.** GTW 7086d, radula. Scale bar = 100  $\mu$ m.



**Figures 182–185.** Distribution maps. All maps Google™ Earth Pro. Image Landsat. © 2017 Google. Data: SIO, NOAA, US Navy, NGA, GEBCO. Inset – general area covered. Not shown – *Chondropomium ignotum*, *Clydonopoma?* *subglobosum*, see text. **182.** *Chondropomium blaincorum* – yellow; *Chondropomium lynx* – purple; *Clydonopoma peasei* – blue; *Clydonopoma polocense* – green; *Clydonopoma punilum* – white; *Clydonopoma titanium* – red square; *Chondropomium sardonys* – red. **183.** *Clydonopoma bahoruense* – purple; *Clydonopoma bartschi* – red; *Chondropomium beatense* – blue; *Chondropomella magnifica* – white; *Clydonopoma nobile* – yellow; *Chondropomella platychilum* – green. **184.** *Chondropomium asymmetricum* – green; *Chondropomium caelicum* – blue; *Clydonopoma bermudezi* – yellow; *Chondropomium gimbense* – purple; *Chondropomium marmoreum* – white; *Chondropomium superbum* – red. **185.** *Chondropomium weinlandi*, “azuense form” – white; barahonense form – red; “weinlandi form” – green. Some dots overlap.

northern shore of the Tiburon Peninsula opposite that island.

**Habitat:** Not reported but Île de la Gonâve is known to be *serie* (an 1818 map labeled it as “sterile et inhabitée”). No live specimens have been recorded. The label to USNM 499359 reads “Point Fantasque... top of first ridge from shore.”

**Other Material Examined (23 Specimens):** **Haiti.** USNM 380245(14), Trou Louise, Île de la Gonâve; USNM 380218(1), USNM 504142(1), Île de la Gonâve; USNM 499359(1), Point Fantasque; USNM 504143(6), Petit-Goâve.

**Variation Among Specimens:** Specimens differ in the strength of the brown patterns with some specimens being almost uniformly white.

**Comparison with Other Species:** The large, polished, turbinoid shell, usually distinctly marked with brown on a white background, is unique in all Hispaniolan annulariids.

**Remarks:** This species is placed in *Clydonopoma* with reservations. No live specimens have been collected and the operculum is unknown. It closely resembles other *Clydonopoma* and *Chondropomium* in sculpture and color patterns. The addition of this species would greatly increase the range of either genus to the west. Only the discovery of the operculum or live material for phylogenetic study will determine its proper place.

**Etymology:** *L. sub-* somewhat + *L. globosum*, round.

***Clydonopoma titanium* new species**  
(Figures 156–160, 182)

**Description:** Shell very large for family (largest adult specimen 29.1 mm length, decollate, including peristome; smallest adult specimen 27.5 mm maximum length, decollate, including peristome), solid, conic, umbilicus wide, surface silky. Protoconch whorls unknown, decollate in adults. Teleoconch of 3.5–4.0 whorls, final whorl adnate except for immediately behind peristome. Suture narrowly but deeply channeled. Peristome single, thick, somewhat reflected, tear drop-shaped, widely expanded but narrowest facing umbilicus, composed of numerous irregular fused lamellae, with or without low auricle posteriorly. Spiral sculpture present as numerous (ca. 45) minute, low feeble threads, most evident as scallops on axial sculpture, more widely spaced in umbilicus. Axial sculpture of numerous (ca. 250) closely spaced, minute threads, gathered in groups of 10–20 between growth lines. Axial lamellae slightly elongated at suture into minute, blade-like cusps, rendering suture finely serrate, no fused tufts. Background color pale tan, orangish, or brownish purple, base paler. Pattern indistinct or bold, of spiral brown bands of “>”-shaped markings and minute dots. Lip usually white, unpatterned. Operculum paucispiral with pseudolamella; pseudolamella covers proximal 75% of opercular whorls exposing underlying corneous base on outer edge. Animal pale cream colored; head with dark grey mottling on top of snout; distal portion of tentacles orange. Radula unknown.

**Type Material:** Holotype: OSUM 42351, 29.1 mm; Paratype 1: OSUM 42352, 27.7 mm; Paratype 2: OSUM 42353, 27.5 mm; Paratype 3: UF 492090, 28.1 mm; Paratype 4: BMSM 121709, 27.9 mm.

**Type Locality:** 775 m elevation, along Rte. 204, ca. 1 km N of Decouze, Département d’Ouest, Haiti, 18.3414° N, –72.5836° W.

**Distribution:** Known only from the type locality.

**Habitat:** Specimens were found on rock piles by the side of the road at ca. 775 m elevation.

**Other Material Examined (5 Specimens):** Haiti. Département d’Ouest. GTW 16816a(5), from the type locality.

**Variation Among Specimens:** Specimens vary in degree of color pattern and background color, which ranges from pale tan to orangish and dark purple-brown.

**Comparison with Other Species:** This species differs from the similar *C. nobile* and *C. poloense* in lacking the channeled suture and in having a much more broadly expanded outer lip.

**Remarks:** This species shares as much in common with taxa such as *Licina habichi* (Weinland, 1862) from western-most Haiti as it does with other *Clydonopoma*. *Licina* species are rare and collections currently lack preserved material for phylogenetic work, but future studies may reassign many of the species now placed in these two genera. We are indebted to José Coltro (Brazil) for calling our attention to this species.

**Etymology:** *G. Titan*, in reference to its size.

### Genus *Superbipoma* new genus

**Type Species:** *Chondropoma superbum* Henderson and Simpson, 1902.

**Description:** Shells large to very large for family (to ca. 35 mm length), elongate-conic, usually decollate. Protoconch of 1.5 smooth, minute whorls. Final whorl detached from previous whorl for ¼–½ turn, forming sharp posterior keel. Axial sculpture of wide, flattened, close-set ribs separated by incised grooves. Spiral sculpture absent on final whorl except present in umbilicus. Overall sculpture appears very smooth, often polished. Suture minutely beaded but lacks fused tufts, deeply channeled. Adult with reflected lip. Lip single or double, but if double inner lip is usually fused to outer lip. Color pattern of bands and blotches, continuous or interrupted; rarely lacking any pattern. Operculum paucispiral with uniform, thin granular deposit. Taenioglossate radula with rachidian tooth, single pair of lateral teeth, and two pairs of marginal teeth. Rachidian and lateral teeth usually unicuspid. Inner marginal deeply multicuspid on outer side. Outer marginal pectinate. Animal with foot longitudinally bisected into lobes. Locomotion ditaxic between lobes of foot. Eyes at base of tentacles; bifid snout produced into short secondary tentacles.

**Distribution:** Rift valley of Hoya de Enriquillo in the Dominican Republic and the Plain du Cul-de-Sac in Haiti.

**Remarks:** This genus differs from *Clydonopoma* and *Chondropomella* in lacking a pseudolamellate operculum and in having deeply incised inner marginal radular teeth. It differs from *Chondropomium* in the expanded lip and greater adult size. The genus is primarily recognized as distinct based on phylogenetic evidence. The included *Superbipoma* species form a group sister to the clade consisting of *Clydonopoma* and *Chondropomium*. Although this position is not strongly supported (Figure 5), it was recovered in all twenty of the independently run analyses and the monophyly of these three genera is strongly supported.

### *Superbipoma asymmetricum* (Pilsbry, 1933) (Figures 161–171, 184)

#### CHRESOXYMY

*Chondropoma* (*Chondropomella*) *asymmetricum* Pilsbry, 1933: 126–127, pl. 9, figs. 4–5.

*Chondropoma* (*Chondropomella*) *enriquillense* Pilsbry, 1933: 127, pl. 9, fig. 1; Bartsch, 1946: 31 [in synonymy of *Chondropoma asymmetricum* Pilsbry, 1933].

*Chondropoma* (*Chondropomium*) *asymmetricum* Pilsbry, 1933: Bartsch, 1946: 31–32, pl. 6, fig. 1.

*Chondropoma* (*Chondropomium*) *inaequilabrum* Bartsch, 1946: 32–33, pl. 5, fig. 6.

*Chondropoma asymmetricum* Pilsbry, 1933: Baker, 1964: 169.

*Chondropoma enriquillense* Pilsbry, 1933: Baker, 1964: 169.

*Chondropomium asymmetricum* (Pilsbry, 1933): Watters, 2006: 62, 152.

*Chondropomium inaequilabrum* (Bartsch, 1946): Watters, 2006: 63, 304–305.

*Chondropomium enriquillense* Pilsbry, 1933: Watters, 2006: 250.

*Chondropomella asymmetricum* (Pilsbry, 1933): Watters and Duffy, 2010: 11.

*Chondropomella inaequilabrum* (Bartsch, 1946): Watters and Duffy, 2010: 11.

**Description:** Shell very large for family (largest adult specimen 33.5 mm maximum length, decollate, including peristome; smallest adult specimen 20.8 mm length, decollate, including peristome), solid, polished, conic, umbilicus open, spire ca.  $\frac{1}{2}$  total length. Protoconch of 1.5 minute, smooth whorls, white with wide tan, central band; protoconch rarely retained in adults. Decollate specimens have jagged, irregular break from earlier whorls, which seems to involve more than just protoconch whorls. Teleoconch of 3.5–3.75 whorls, final whorl distinctly detached for last  $\frac{1}{4}$ th of whorl and deflected anteriorly. Suture narrow, deeply channeled. Peristome double, tear drop-shaped. Inner lip not erect, fused to outer lip. Outer lip expanded, narrowest facing umbilicus, non-auriculate, distinctly detached from previous whorl, forming sharp posterior keel. Spiral sculpture absent except for few very weak, almost obsolete cords within umbilicus. Axial sculpture of flattened, low ribs, separated by incised grooves, ca. 200–250 ribs on final whorl, each forming minute bead at suture; no fused tufts present. Background color very variable, from white to tan, with axial zig-zag brown markings arranged in vague spiral bands; umbilicus white. Outer lip usually white, rarely banded. Shell rarely uniformly white. Operculum paucispiral with thin calcareous deposit. Radula as in genus. Animal uniformly pale tan or white with dark band at base of snout.

**Type Material:** *Chondropoma asymmetricum* Pilsbry, 1933: Lectotype: ANSP 46656; Paralectotypes: ANSP 373761(4); USNM 426041(1). *Chondropoma enriquillense* Pilsbry, 1933: Holotype: ANSP 146715. *Chondropomium inaequilabrum* (Bartsch, 1946): Holotype: USNM 471939.

**Type Locality:** *Chondropoma asymmetricum* Pilsbry, 1933: “Fond Parisien, on the south shore of Étang Saumâtre, Haiti.” *Chondropoma enriquillense* Pilsbry, 1933: “Lake Enriquillo, Santo Domingo.” Collected by Bond... James Bond in 1928. *Chondropomium inaequilabrum* (Bartsch, 1946): “Mount Petitchemin, Department de l’Ouest, Haiti.”

**Type Figured:** *Chondropoma asymmetricum* Pilsbry, 1933: Pilsbry, 1933, pl. 9, figs. 4, 5. *Chondropoma enriquillense* Pilsbry, 1933: Pilsbry, 1933, pl. 9, fig. 1. *Chondropomium inaequilabrum* (Bartsch, 1946): Bartsch, 1946, pl. 5, fig. 6.

**Distribution:** Found below 500 m elevation in the northern foothills of the Sierra Baoruco in the rift valley of Hoya de Enriquillo/Plain du Cul-de-Sac facing the

south shores of Lago Enriquillo and Étang Saumâtre. Not recorded from the northern portion of the valley, where it is replaced by *S. superbum*. *Chondropoma inaequilabrum* Bartsch, 1946, was described from the Haitian Department de l’Ouest from Mount Petitchemin. This location is not listed among the 651 peaks in Haiti by [www.peakery.com](http://www.peakery.com) and we have not been able to locate it. The Department de l’Ouest includes the Plain du Cul-de-Sac and, like most species in the genus, this taxon probably originated from that rift valley as well.

**Habitat:** Under fossilized coral rubble in xeric areas with agave and cacti. Often common.

**Other Material Examined (265 Specimens): Haiti.**

**Département d’Ouest.** USNM 471937(1), Fond Parisien; UF 32148(20), UF 32149(25), 4 km S of Fond Parisien; UF 32162(21), 10 km SSE of Fond Parisien; USNM 426041(1), S shore Étang Saumâtre; **Dominican Republic. Independencia Province.** OSUM 42369(15), 466 m, 1.3 km E of center of Puerto Escondido, 18.3290° N, –71.5593° W; OSUM 42357(9), avocado grove, just outside Puerto Escondido; UF 216858b(24), 430 m, S km WNW of Puerto Escondido; UF 216859(13), 490 m, 11 km WNW of Puerto Escondido; UF 216651(3), 275 m, 12 km WNW of Puerto Escondido; OSUM 42370(42), 473 m, along RD 541, 2.3 km NNW of El Naranjo, 18.3514° N, –71.6279° W; OSUM 42375(20), 224 m, hill top between Jimaní and El Limón, off RD 46, 18.4504° N, –71.8115° W; UF 216851a(12), 210 m, 5 km SW of El Limón; UF 216857(15), 40 m, 2 km NW of El Limón; UF 216652(1), 6.2 km SE of Jimaní; UF 216855a(29), UF 216862b(25), 7 km SE of Jimaní; GTW 16218d(9), ridge NW of Jimaní; GTW 16023a(5), 1.2–2 km E of Jimaní.

**Variation Among Specimens:** Specimens vary in the degree of the outer lip expansion and the depth of the color pattern, which ranges from nearly all white to heavily mottled with brown.

**Comparison with Other Species:** This species differs from the similar *S. superbum* in being less elongate and in having the color pattern consist of axially arranged zig-zags, whereas in *S. superbum* the pattern is of interrupted spiral bands.

**Remarks:** Watters and Duffy (2010) placed this species in *Chondropomella*. However, it lacks the highly modified, calcareous operculum of that genus. *Chondropomium inaequilabrum* (Bartsch, 1946) was differentiated from *C. asymmetricum* only by size but it falls well within the variation of this species.

**Etymology:** *Chondropoma asymmetricum* Pilsbry, 1933: *L. asymmetricus*, asymmetrical [outer lip]. *Chondropoma enriquillense* Pilsbry, 1933: Lago Enriquillo, Dominican Republic. *Chondropomium inaequilabrum* (Bartsch, 1946): *L. inaequi-*, unequal + *L. labrum*, lip. The outer lip is unequally expanded around the aperture.

***Superbipoma superbum* (Henderson and Simpson, 1902)**

(Figures 172–181, 184)

## CHRESOONYMY

*Chondropoma superbum* Henderson and Simpson, 1902: 88–89, text. fig.; Parodiz and Tripp, 1988: 149; McGhie, 2008: 31.

*Chondropoma* (*Chondropomium*) *weinlandi superba* Henderson and Simpson, 1902. Henderson and Bartsch, 1920: 60.

*Chondropoma* (*Chondropomium*) *superbum* Henderson and Simpson, 1902; Clench and Aguayo, 1937: 64; Bartsch, 1946: 23–24, pl. 5 fig. 1.

*Chondropomium superbum* (Henderson and Simpson, 1902): Watters, 2006: 63, 498.

**Description:** Shell large for family (largest adult specimen 29.3 mm maximum length, decollate, including peristome; smallest adult specimen 20.1 mm length, decollate, including peristome), polished, almost translucent, conic to fairly high-spired, umbilicus open, spire  $\frac{1}{2}$ – $\frac{1}{3}$  total length. Protoconch of 1.5 minute, smooth, white whorls, decollated in adults. Decollate specimens have jagged, irregular break from earlier whorls, which seems to involve more than just protoconch whorls. Teleoconch of 3.25–4.25 whorls, final whorl distinctly detached for last  $\frac{1}{4}$ th of whorl and deflected anteriorly. Suture narrow, deeply channeled. Peristome single, tear drop-shaped. Lip expanded, narrowest facing umbilicus, with minute triangular posterior auricle, distinctly detached from previous whorl, forming sharp posterior keel. Spiral sculpture absent except for few very weak, almost obsolete cords within umbilicus. Axial sculpture of flattened, low ribs, separated by incised grooves, often grouped in growth series, ca. 160 ribs on final whorl, each forming minute bead at suture; no fused tufts present. Background color very variable, from white to tan to purplish brown, early whorls often darker; axial spots and dashes axially aligned on trailing edge of growth series, rarely without marks, rarely with continuous or nearly so spiral bands; lip and umbilicus white. Operculum paucispiral with thin calcareous deposit. Radula as in genus.

**Type Material:** Holotype: USNM 168798; Paratypes: ANSP 386772(44); UF 119090(2); UF 119165(4); UF 119169(6); UF 22229(33), UF 22230(4); Manchester Museum (UK); EE.3688(4), listed as syntypes, see McGhie (2008); CMNH 62.38661(6), listed as syntypes.

**Type Locality:** “On a high limestone hill back of Thomazeau, Haiti.”

**Type Figured:** Henderson and Simpson, 1902, text fig.

**Distribution:** Throughout the Hoya de Enriquillo/Plain du Cul-de-Sac from north of Port-au-Prince to the NW shores of Lago Enriquillo. It occurs at and below sea level

(Lago Enriquillo is below sea level), rarely to ca. 600 m. It has not been found along the southern shore of Lago Enriquillo where it is replaced by *S. asymmetricum*. Locally common.

**Habitat:** Under fossilized coralline debris and in rock piles in xeric areas with agave and cacti. Locally common. Co-occurs with *C. weinlandi*, *C. magnificum* (Pfeiffer, 1854), and *Crosseopoma vermiculatum s.l.* (Bartsch, 1946).

**Other Material Examined (406 Specimens): Haiti.**

**Département de l'Ouest.** UF 33813(16), 14 km SE of Duvalierville [Cabaret]; UF 31983(2), 18 km SE of Duvalierville [Cabaret]; UF 32090(6), 350 m, 11 km NNE of Beudet; UF 119090(2), UF 119165(4); UF 119169(6), UF 183694(44), UF 22229(33), UF 22230(4), Thomazeau; UF 32559(7), 2 km E of Thomazeau; UF 32565(25), UF 32726(1), 50 m, 5 km W of Thomazeau; UF 32041(1), 24 km SSW of Mirebalais; UF 32052(5), 25 km SSW of Mirebalais. **Département du Centre.** GTW 7086f(7), 632 m, Fond Cavalier, 18.7164° N, –72.1658° W. **Dominican Republic. Independencia Province.** UF 216860(5), 2 km E of La Lajas; UF 216852(44), 6 km SE of La Lajas; GTW 7086a(1), OSUM 42360(9), Bartolomé, N shore of Lake Enriquillo; GTW 7087i(1), Boca de Cachón; GTW 7086b(34), old quarry, off RD 48, 1.8 km ESE of Boca de Cachón, 18.5514° N, –71.8232° W; UF 216853(35), UF 216856(13), 7 km NW of Boca de Cachón; GTW 7086c(7), 4.7 km S of Boca de Cachón, 18.5129° N, –71.8440° W; GTW 7086d(16), Boca de Cachón; UF 216854(7), 2 km NNW of La Descubierta; UF 216849(37), 250 m, 6 km NE of La Descubierta; UF 216826a(19), 7 km E of La Descubierta; UF 216825(18), 6 km NW of Postrer Río.

**Variation Among Specimens:** This species is much more varied in color than described by either Henderson and Simpson (1922) or Bartsch (1946). The degree of background color ranges from nearly all white to nearly all brown or purplish-brown; the strength of the axial markings varies from small spots or dashes to nearly complete spiral bands.

**Comparison with Other Species:** See under *S. asymmetricum*.

**Etymology:** *L. superbum*, superb.

## DISCUSSION

The relationships within and among annulariid species groups are more fully understood when mutually informed by morphology and phylogeny. While *Chondropomium* and *Superbipoma* share features that have been historically used to define genera, the well-supported position of the interloping *Clydonopoma* species group suggest that sharing these features does not necessarily indicate a close relationship. Likewise, while

**Table 1.** Specimens used in phylogenetic analyses and associated GenBank accession numbers for each sequence. New sequences generated for this study are in **boldface**. DR = Dominican Republic.

ITS	12S	16S	COI	Collection #	Taxon	Locality
		KX496786	KX496708	GTW 7451b	<i>Pomatias rivulare</i> (Eichwald, 1829)	Szekeşárd, Hungary
		KX49784	KX496707	GTW 6987h	<i>Pomatias elegans</i> (Müller, 1774)	Órtilos, Hungary
	<b>KX890243</b>	<b>KX890244</b>		GTW 15254a	<i>Abbottella milleacantha</i> Watters and Duffy, 2010	Guaragua, DR
<b>KX863632</b>	<b>KX863589</b>	<b>KX863655</b>	<b>KX863609</b>	GTW 16031b	<i>Chondropomella magnificum</i> (Pfeiffer, 1852)	Puerto Escondido, DR
<b>KX863633</b>	<b>KX863590</b>		<b>KX863610</b>	GTW 7086e2	<i>Chondropomella magnificum</i> (Pfeiffer, 1852)	Bartolomé, DR
<b>KX863634</b>	<b>KX863591</b>	<b>KX863656</b>	<b>KX863611</b>	GTW 7087h	<i>Chondropomium weinlandi</i> (Pfeiffer, 1862) [ <i>azuense</i> ]	Bartolomé, DR
<b>KX863636</b>	<b>KX863593</b>	<b>KX863658</b>	<b>KX863613</b>	GTW 7087z	<i>Chondropomium weinlandi</i> (Pfeiffer, 1862)	Bartolomé, DR
<b>KX863622</b>	<b>KX863579</b>	<b>KX863645</b>	<b>KX863600</b>	GTW 7087u	<i>Chondropomium weinlandi</i> (Pfeiffer, 1862)	Bartolomé, DR
<b>KX863623</b>	<b>KX863580</b>	<b>KX863646</b>		GTW 7087q	<i>Chondropomium weinlandi</i> (Pfeiffer, 1862)	Bombita, DR
<b>KX863625</b>	<b>KX863581</b>	<b>KX863648</b>	<b>KX863602</b>	GTW 7087t	<i>Chondropomium weinlandi</i> (Pfeiffer, 1862)	El Limón, DR
<b>KX863624</b>		<b>KX863647</b>	<b>KX863601</b>	GTW 7087l	<i>Chondropomium weinlandi</i> (Pfeiffer, 1862)	Galindo Adrento, DR
	<b>KX863577</b>	<b>KX863643</b>	<b>KX863598</b>	GTW 7087o	<i>Chondropomium weinlandi</i> (Pfeiffer, 1862) [ <i>barahonense</i> ]	Bombita, DR
<b>KX863642</b>	<b>KX863597</b>	<b>KX863664</b>	<b>KX863618</b>	GTW 7087v	<i>Chondropomium weinlandi</i> (Pfeiffer, 1862) [ <i>azuense</i> ]	Bombita, DR
<b>KX863621</b>	<b>KX863578</b>	<b>KX863644</b>	<b>KX863599</b>	GTW 7087y	<i>Chondropomium weinlandi</i> (Pfeiffer, 1862) [ <i>barahonense</i> ]	Bombita, DR
<b>KX863641</b>	<b>KX863596</b>	<b>KX863663</b>	<b>KX863617</b>	GTW 16524a	<i>Clydonopoma bahoruense</i> (Bartsch, 1946)	Angostura, DR
<b>KX863626</b>	<b>KX863582</b>	<b>KX863649</b>	<b>KX863603</b>	GTW 7089d	<i>Clydonopoma nobile</i> (Pfeiffer, 1852)	Virgen de San Rafael, DR
<b>KX863627</b>	<b>KX863583</b>	<b>KX863650</b>	<b>KX863604</b>	GTW 16226b	<i>Clydonopoma polocense</i> (Bartsch, 1946)	Carbon de Polla, DR
<b>KX863638</b>		<b>KX863660</b>	<b>KX863614</b>	GTW 7088b	<i>Crossepoma vermiculatum domingoense</i> (Bartsch, 1946)	Oviedo, DR
	<b>KX863586</b>	<b>KX863653</b>	<b>KX863607</b>	GTW 7088in	<i>Crossepoma vermiculatum domingoense</i> (Bartsch, 1946)	Cabral, DR
<b>KX863628</b>	<b>KX863584</b>	<b>KX863651</b>	<b>KX863605</b>	GTW 7088l	<i>Crossepoma vermiculatum domingoense</i> (Bartsch, 1946)	Carbon de Polla, DR
<b>KX863629</b>	<b>KX863585</b>	<b>KX863652</b>	<b>KX863606</b>	GTE 7088i	<i>Crossepoma vermiculatum domingoense</i> (Bartsch, 1946)	Rio Palomino, DR
<b>KX863630</b>	<b>KX863587</b>	<b>KX863654</b>	<b>KX863608</b>	GTW 7088o	<i>Crossepoma vermiculatum domingoense</i> (Bartsch, 1946)	El Limón, DR
<b>KX863637</b>	<b>KX863594</b>	<b>KX863659</b>		GTW 16218c	<i>Superbipoma asymmetricum</i> (Pilsbry, 1933)	El Limón, DR
<b>KX863640</b>	<b>KX863595</b>	<b>KX863662</b>	<b>KX863616</b>	GTW 16218b	<i>Superbipoma asymmetricum</i> (Pilsbry, 1933)	El Naranjo, DR
<b>KX863639</b>		<b>KX863661</b>	<b>KX863615</b>	GTW 16218a	<i>Superbipoma asymmetricum</i> (Pilsbry, 1933)	Puerto Escondido, DR
<b>KX863631</b>	<b>KX863588</b>			GTW 16023b	<i>Superbipoma asymmetricum</i> (Pilsbry, 1933)	Puerto Escondido, DR
<b>KX863635</b>	<b>KX863592</b>	<b>KX863657</b>	<b>KX863612</b>	GTW 7087jl	<i>Superbipoma superbium</i> (Henderson & Simpson, 1902)	Bartolomé, DR

branch lengths between genera (e.g., *Clydonopoma* and *Chondropomium*) are similar to or shorter than some of those within a genus (i.e. *Superbipoma*), these same characters provide justification for not combining all three genera into a single large taxon. At the species level, our phylogenetic results have implications for putative

subspecies or morphotypes. In particular, the two individuals of *Chondropomium weinlandi* “azuense form” highly supported relationships with two individuals of different types (i.e., with *C. weinlandi* with 99% bootstrap support and with *C. weinlandi* “barahonense” with 94% bootstrap support). Similarly, *C. weinlandi* “barahonense”

individuals are not most closely related, with high support. These results are consistent with a single polymorphic species rather than multiple separate species or subspecies.

Although *Chydronopoma*, *Chondropomella*, and other Tiburon genera have a heavily calcified and complex pseudolamellate operculum, this has been reduced to a fine granular deposit in *Chondropomium* and *Superbipoma*. This follows the findings of Skomrock (2014), which suggested that a calcified operculum was the ancestral condition of the Annulariidae. Taxa lacking calcification have secondarily lost this feature and are representative of a derived condition. It appears that the pseudolamella was lost in *Chondropomium* and *Superbipoma* from a pseudolamellate ancestor. Both of these genera are lowland forms but it is not clear how (or if) the loss of the pseudolamella is associated with that change in habitat.

*Crosseopoma vermiculatum* (Bartsch, 1946) is conchologically very similar to *Chondropomium* and is often sympatric with *C. weinlandi*. Described as a *Chondropomium*, Watters (2012) moved it to *Crosseopoma* Bartsch, 1946, based on the structure of the operculum. Although *Crosseopoma* is not reviewed here, *C. vermiculatum* is confirmed as belonging to a genus apart from *Chondropomium*. However, *C. vermiculatum* is not the type species of the genus *Crosseopoma* (= *Chondropoma emilianum* Weinland, 1862) and additional work is needed to determine the relationship of *Crosseopoma* to *Chondropomium*.

It is of interest to note which groups have “broken out” of the Tiburon Peninsula to begin colonization of the remainder of Hispaniola since the Miocene. *Chydronopoma* is apparently limited to the mesic uplands of the Sierra de Baoruco and may be ecologically restricted from establishing itself in other mountain ranges by virtue of the intervening xeric lowlands. *Chondropomium*, *Chondropomella*, and *Superbipoma*, on the other hand, prefer these xeric lowland habitats and have spread up the rift valley and connecting river valleys (in *Chondropomium*) into adjacent Hispaniola, all the while remaining lowland forms. Only *C. caelicum*, which has advanced the furthest into Hispaniola, has colonized a more montane habitat.

This study confirms the narrow endemism of some Tiburon genera and probably is representative of annulariid taxa in general. It also demonstrates the utility of the phylogenetic study of this group to determine not only genus-level patterns but also patterns within a species. Unfortunately, the great majority of specimens in collections consist of material unsuitable for phylogenetic work, including this study. Coupled with the endemism of most taxa, future phylogenetic work on the group would require extensive resampling on a fine scale that may not be possible due to time, financial, and political constraints, as well as the possibility of taxa having become extirpated or even extinct.

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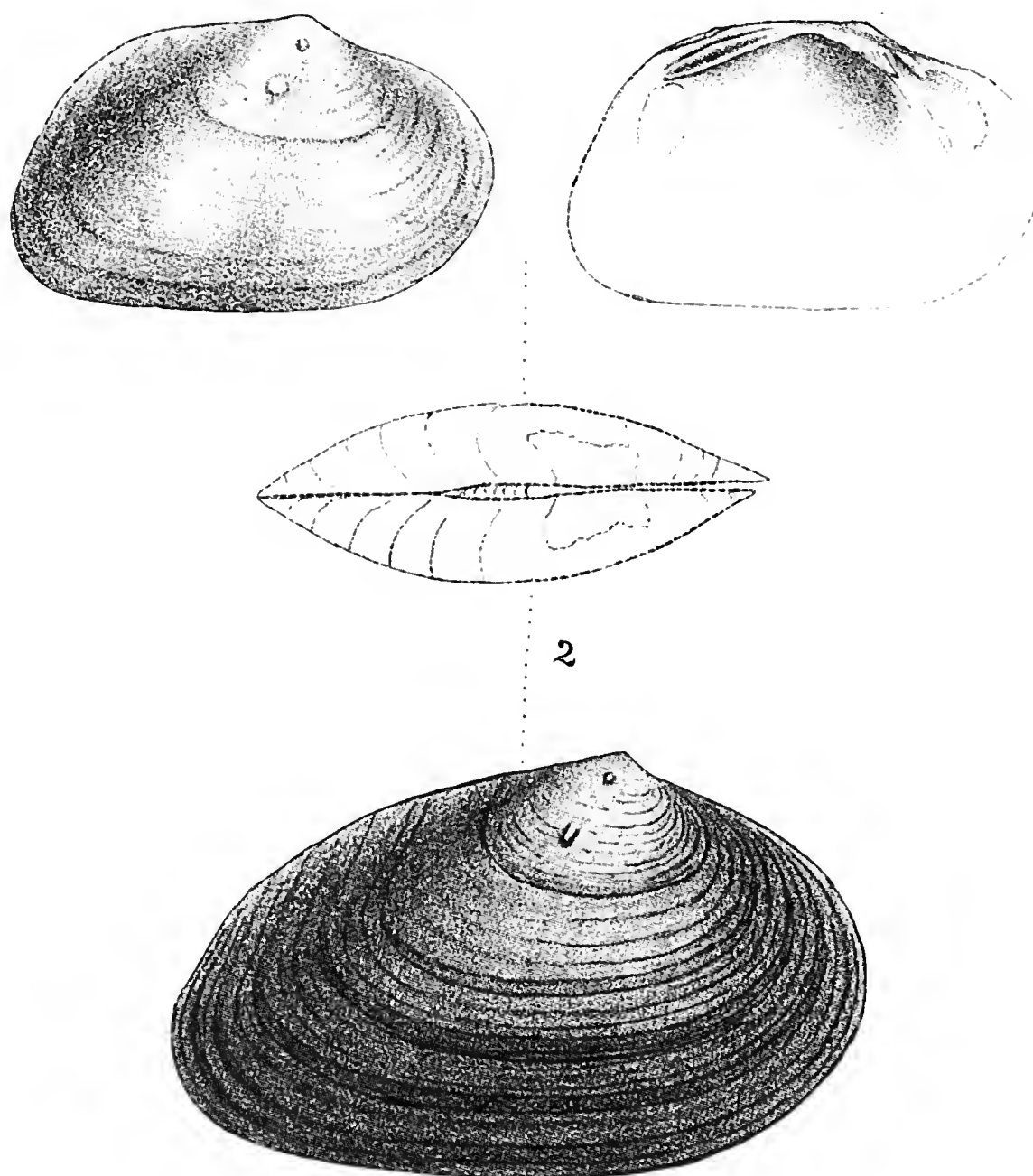
## Note

### Designation of a lectotype for *Parvaspina collina* (Conrad, 1836) (Bivalvia: Unionidae)

Perkins et al. (2017) erected a new genus, *Parvaspina*, for two species with spines formerly placed in *Elliptio* and *Pleurobema*. Based on genetic information, *Elliptio steinstausana* (Johnson and Clarke, 1983) and *Pleurobema collina* (Conrad, 1836) were transferred to *Parvaspina*.

*Unio collinus* Conrad, 1837[sic] was designated the type species of the new genus (Perkins et al., 2017). They noted the lectotype was ANSP 41007. They did not cite the revisionary work of Johnson (1970) nor mention the lectotype designation as presented by Johnson and Baker (1973:151) or Graf and Cummings (2017).

In his Monography, Conrad (1835–1840), figured what appears to be three specimens of *Unio collinus* before the text description was published (Conrad, 1836f (No. 7): pl. 36, fig. 2). This plate is dated 1836, so the taxon takes this



1. *Unio occidentalis*, C. 2. *U. collinus*, Con.

Figure 1. Original illustrations of *Unio collinus* in Conrad (1836: pl. 36 fig. 2).

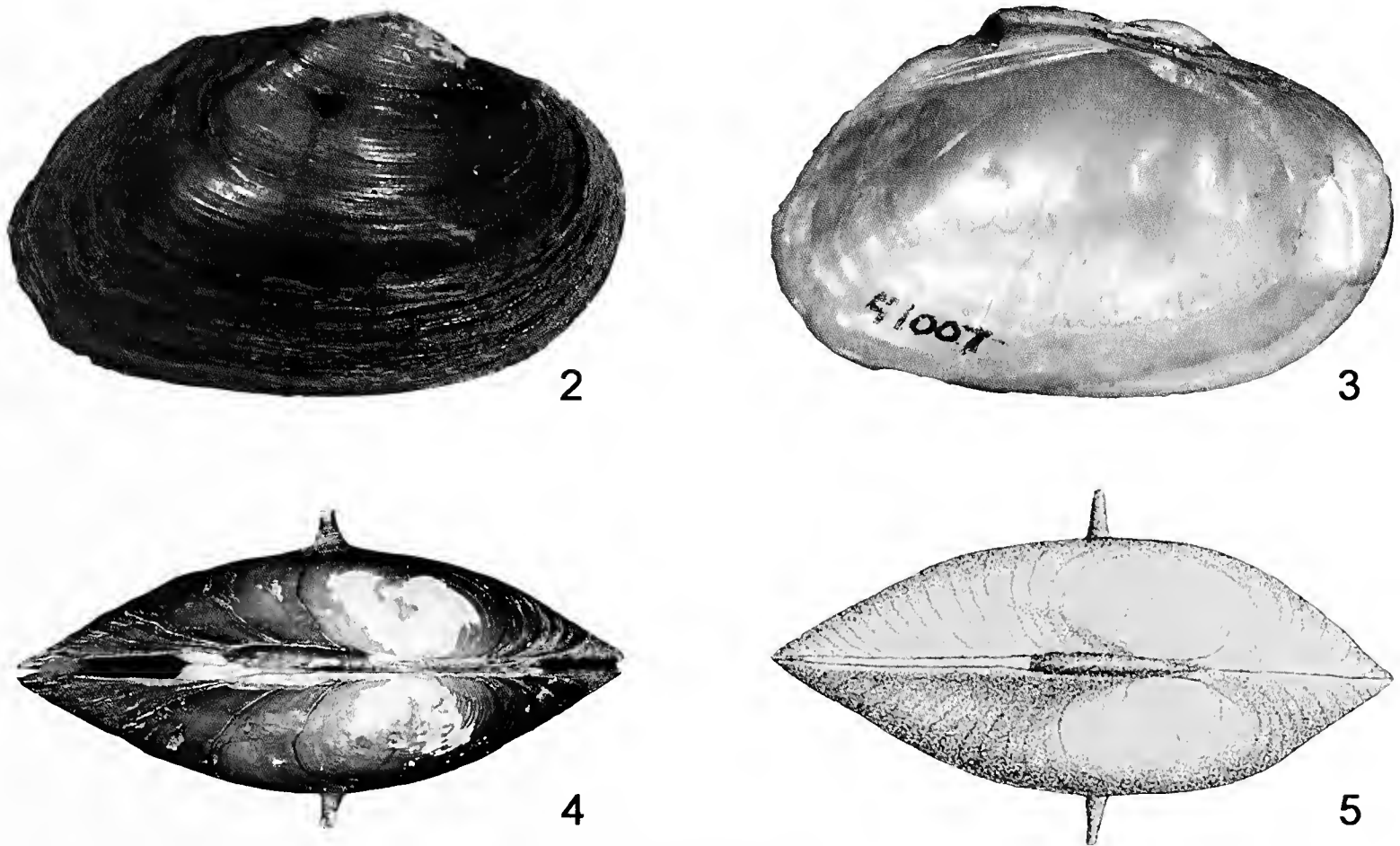
date of publication. This is an indication and is the first use of the name *Unio collinus*. Conrad's pl. 36, fig. 2 (Figure 1) is interpreted as representing all three of his original syntype specimens: the two figures in the top row are one specimen; the dorsal view in the middle row shows an eroded umbo area without any evidence of spines is a second specimen and the bottom figure of the outside of the right valve is the third specimen.

**Lectotype Designation:** Conrad (1837a (No. 8):65) in the Monography described *Unio collinus* and mentioned he had three specimens and referred to pl. 36, fig. 2, citing the catalog number "Cab. ANSP No. 20408". Subsequently, he remarked "since the publication of this species in a former number of this work, I have received a few specimens from the same locality with the first described, which present the very remarkable character of spines" (Conrad, 1840a (No. 12):109–110, pl. 60, fig. 3). No catalog number was listed for these new specimens. One of these new specimens was figured in pl. 60, fig. 3 (Conrad 1840a) (Figure 5). The problem is that the specimens later received and figured are topotypes identified by the author of the species, not part of the original type series (See Articles 74.1; 74.2). Johnson (1970: 300) noted the type lot, ANSP 20408, was lost and observed "this subsequently figured metatype, here selected, lectotype ANSP 41007." The IUCN Code does not recognize the term *metatype*. This topotypic lot was not part of the original type series and as such cannot be used as a source for

designating a lectotype. Therefore, Johnson's (1970) lectotype designation is invalid. The original figure of Conrad (1836f: pl. 36, fig. 2) can be used to designate the lectotype even if the specimens are lost (see Code Articles 74.1, 74.2, 74.4). Fig. 2 of pl. 36, assigned museum number ANSP 20408, represents the valid syntype series, even if the specimens are lost. **The top two valves in Conrad's fig. 2 (see Figure 1) are here designated the lectotype for *Unio collinus* Conrad, 1836 (see Code Article 74.4).**

The catalog number ANSP 20408 was listed for the original type series by Conrad (1837a:65). This number is not a Malacology Department number. The ANSP Malacology Department did not begin assigning catalog numbers until 1889. The invalid lectotype ANSP 41007 is in the collection and identified as *Unio collinus*. Rosenberg remarked "I suspect that there was an early ledger where catalogue numbers were assigned to items across the Academy, since in the 1830's we didn't have formal departments. If there was such a ledger, however, it no longer exists." (Gary Rosenberg, Pers. Comm.).

*Parvaspina collina*, ANSP 41007, was designated as a lectotype (Figures 2–4), but does not match any of the original figures by Conrad (Figure 1), more closely resembling the subsequent figure by Conrad (see Figures 4 and 5). The ANSP 41007 specimen has Rockbridge County written in pencil on the inside of the left valve, and has some dried tissue on the inside of the shell (Figure 3), but lacks a catalog number written in the shell. Rockbridge County is



**Figures 2–5.** *Parvaspina collina* (Conrad) ANSP 41007 invalid lectotype. 2. External surface of right valve. 3. Internal surface of left valve. 4. Dorsal view of paired valves. 5. Original illustration of *Unio collinus* in Conrad (1840: pl. 56, fig. 3).

listed in the type locality. It has been suggested that the specimen catalogued today as ANSP 41007 was part of the original type series. However, comparison of the valves of the ANSP 41007 specimen (Figures 2–4) with the illustration of Conrad's type figures (Figure 1), makes it clear that the catalogued specimen was not one originally illustrated in Conrad's pl. 36 fig. 2 (Figure 1). It does resemble Conrad's later pl. 56, fig. 3 (Figure 5). This being the case, then ANSP 41007 is a topotype and not part of the original type series.

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## Notice

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### FLORIDA UNITED MALACOLOGISTS 2018

The ninth meeting of Florida United Malacologists (FUM 2018) will take place on Saturday, January 27, 2018, at the Bailey-Matthews National Shell Museum on Sanibel Island, Florida. The one-day gathering brings together researchers, citizen scientists, and students interested in a broad swath of mollusk-related topics. FUM follows the pattern of similar informal gatherings such as BAM (Bay Area Malacologists), SCUM (Southern California United Malacologists), MAM (Mid-Atlantic Malacologists), and OVUM (Ohio Valley United Malacologists). The event circulates among different Florida organizations, but usually takes place at the Shell Museum every other year. Presentations are limited to 15 minutes plus 5 minutes for questions. Presenters are required to submit a brief abstract limited to 150 words or less. The gathering will be free to presenters and pre-registered participants. Box lunches and dinner at a local restaurant (to be arranged) will be available to participants and presenters. The deadline for abstract submission is December 31, 2017.

For registration and further information, visit <http://shellmuseum.org/about/news/florida-united-malacologists-2018>, or email [jleal@shellmuseum.org](mailto:jleal@shellmuseum.org).

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## INSTRUCTIONS TO AUTHORS

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*The Nautilus* publishes articles on all aspects of the biology, paleontology, and systematics of mollusks. Manuscripts describing original, unpublished research and review articles will be considered. Brief articles, not exceeding 1000 words, will be published as Research Notes and do not require an abstract.

**Manuscripts:** Each original manuscript and accompanying illustrations should be submitted to the editor via e-mail. Authors should follow the general recommendations of Scientific Style and Format—The CSE Manual for Authors, Editors, and Publishers, available from the Council of Science Editors at <http://www.scientificstyleandformat.org/Home.html>.

The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Metric, not English, units are to be used. The sequence of sections should be Title, Author(s) and Affiliations, Abstract, Additional Keywords, Introduction, Materials and Methods, Results, Discussion, Conclusions, Acknowledgments, Literature Cited, Tables, Figure Captions, Figures. If the author for correspondence is not the senior author, please indicate in a footnote. The abstract should summarize in 250 words or less the scope, main results, and conclusions of the article. Abstracts should be followed by a list of additional keywords. All references cited in the text must appear in the Literature Cited section and vice-versa. Please follow a recent issue of *The Nautilus* for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included within the pagination of cited work. Tables must be numbered and each placed on a separate page. If in doubt, please follow a recent issue of the journal for sequence of sections and other style requirements.

**Illustrations:** Illustrations are rendered either at full-page width (maximum width 17 cm) or column width (maximum width 8.2 cm). Please take these dimensions into consideration when preparing illustrations. Page-width illustrations ideally should span the entire width of printed page (17 cm). "Tall" page-width illustrations should be avoided, square or "landscape" formats work better. Please design plates accordingly, such that there will be enough space left at the bottom of printed page for plate caption. (Digital technology has made this task much easier.)

All line drawings must be in black, clearly detailed, and completely labeled. Abbreviation definitions must be included in the caption. Line drawings must be high resolution files at least 600 dpi (dots per inch) resolution at actual size. Standard digital formats for line drawings include .tif, .bmp, .psd, .eps, and .pdf.

Photographs may be submitted in black-and-white or color, preferably in RGB mode if in color. Standard digital formats for photographs include .tif, .psd, .jpg, or .pdf. Photographs must be high resolution files at least 300 dpi resolution at actual (printed) size.

If more than one figure is included in an illustration, all figures are to be consecutively numbered (Figures 1, 2, 3, . . . , NOT Figures 1A, 1B, 1C, . . . , NOR Plate 1, Figure 1, . . . ). In illustrations with more than one figure, make sure that blank areas between figures should be kept to a minimum, thereby allowing for more area for each individual figure.

Compressed (e.g., .jpg) or other low-resolution file formats may be used to facilitate original submission and the review process, but may not be acceptable at final submission (see below).

**Types and Voucher Specimens:** Deposition of the holotype in a recognized institutional, public collection is a requirement for publication of articles in which new species-level taxa are described. Deposition of paratypes in institutional collections is strongly recommended, as is the deposition of representative voucher specimens for all other types of research work.

**The Editorial Process:** Upon receipt, all manuscripts are assigned a number and acknowledged. The editor reserves the right to return manuscripts that are substandard or not appropriate in scope for journal. Manuscripts deemed appropriate for the journal will be sent for critical review to at least two reviewers. The reviewers' recommendations will serve as basis for rejection or continuation of the editorial process. Reviewed manuscripts will be sent back to authors for consideration of the reviewers comments. The revised version of the manuscript may at this point be considered accepted for publication by the journal.

**Final Submission:** Authors of accepted manuscripts are required to submit a final version to the editor at [jleal@shellmuseum.org](mailto:jleal@shellmuseum.org). High-resolution image files may be sent to the editor at this stage.

**Proofs:** After typesetting, proofs will be sent to the author. Author should read proofs carefully and send corrections to the editor within 48 hours. Changes other than typesetting errors will be charged to the author at cost.

**Offprints:** An order form for offprints will accompany the proofs. Offprints will be ordered directly from the editor. Authors with institutional, grant, or other research support will be asked to pay for page charges at the rate of \$60 per page.

More information at <http://shellmuseum.org/learn/the-nautilus>.

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